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Journal of the Royal Society of Western Australia

MUSEUM VICTORIA
25 SEP 1998

Centennial Issue
1897 - 1997

Mueller Botanic Society of Western Australia
West Australian Natural History Society
Natural History and Science Society of Western Australia
Royal Society of Western Australia

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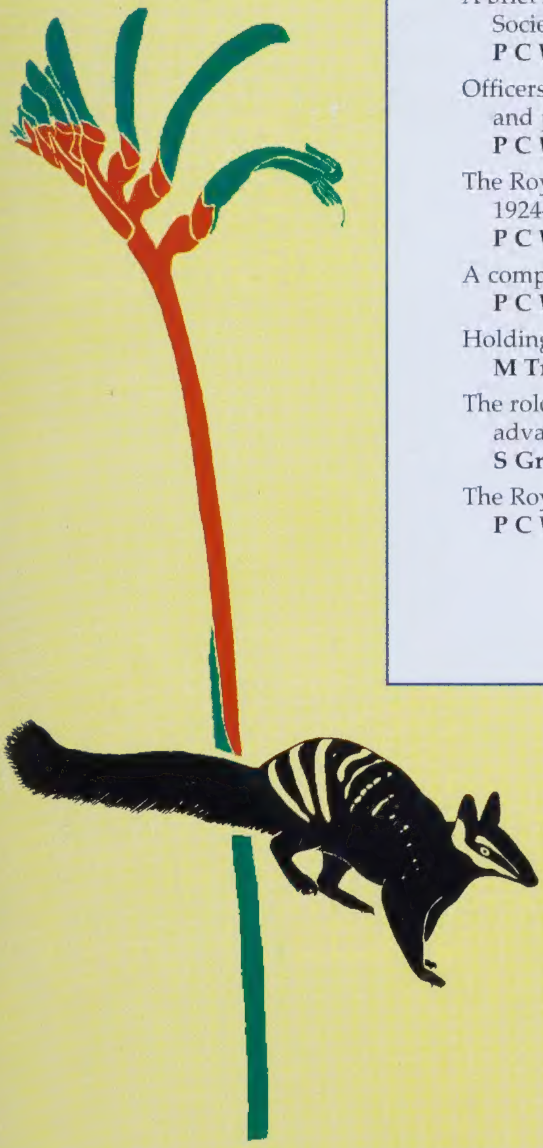

Volume 81 Part 1
March 1998

ISSN 0035-922X

The Royal Society of Western Australia

To promote and foster science in Western Australia

Patron

Her Majesty the Queen

Vice-Patron

His Excellency Major General Michael Jeffery AD MC
Governor of Western Australia

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The Royal Society of Western Australia was founded in 1914. The Society promotes exchange among scientists from all fields in Western Australia through the publication of a journal, monthly meetings where interesting talks are presented by local or visiting scientists, and occassional symposia or excursions on topics of current importance. Members and guests are encouraged to attend meetings on the third Monday of every month (March - December) at 8 pm Kings Park Board offices, Kings Park, West Perth, WA 6005.

Individual membership subscriptions for the 1997/1998 financial year are $40 for ordinary Members and $20 for Student and Associate Members. Library, company and institution subscriptions are $60 for the 1996 calendar year. For membership forms, contact the membership Secretary, ℅ W A Museum, Francis Street, Perth, WA 6000.

The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences ambraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

Foreword from the President of the Royal Society of Western Australia

On behalf of the council of the Royal Society of Western Australia, it gives me great pleasure to introduce this historic Centennial Issue of the Journal of the Society. This volume provides a unique compilation of the history of the Society - from the early days, starting in 1891 with the Western Australian Natural History Society, which provided the foundation for the Mueller Botanic Society in 1897. It is from the latter Society that the Royal Society of Western Australia eventually evolved in 1913, and the Royal Society has continued to promote Science in Western Australia to the present day.

This Centennial Issue documents the early history of the Society, the members of Council, the Presidents and Vice-Presidents, from 1900 to the present day. The Royal Society Medal, founded to commemorate the centenary of the birth of the famous scientist Lord Kelvin, was first designed and struck in 1924, and a complete list of outstanding scientists who have contributed to science in Western Australia and who have been awarded this medal, is provided here.

This volume also provides a complete bibliography of articles and authors of articles published in the Journal of the Royal Society of Western Australia and precursor journals. This provides a unique resource to locate articles, subjects and authors.

The Royal Society of Western Australia also maintains an important collection of books, journals and other scientific literature, much of which is unique. These holdings are housed in the Western Australian Museum, and are available for access. A complete inventory of the RSWA library holdings is presented here.

As befits a special centenary edition, this volume also includes an article on the role of the Royal Society in the advancement of Science in Western Australia. This article charts some of the highlights of RSWA contributions to Science in WA and the changing role of the Society with time. For example, the Society has promoted the establishment of reserves for flora and fauna, has commented on urban planning, land management issues, heritage issues, conservation, forestry, the Perth Observatory, the EPA and made submissions on Science policy development to the State Government. The article also analyses the present function of the Society, and proposed strategies to ensure that the Society stays relevant and vibrant for the next century. This is an important aspect - any organisation must adapt to changing times, and the times are certainly changing more rapidly now than ever before.

I commend this volume to you as a major resource and an outstanding record of the activities of the Royal Society of Western Australia over the past century. I thank those involved for its production.

We all look forward to the next century of the Society.

MUSEUM VICTORIA
25 SEP 1998

Professor Mike Jones
President

Centennial Issue, Volume 81

Journal of the Royal Society of Western Australia, 81:1-4, March 1998

A brief history of the Journals, Crests, Medal and Seal of the Royal Society of Western Australia and previous Societies, 1897-1997

The History of the Royal Society of Western Australia was described by an unpublished manuscript of W M Traylen (1924) and a Presidential Address of C F H Jenkins (1965), and addressed in passing by Summers (1982). These historical accounts briefly covered the various societies which were the forerunners to the Royal Society of Western Australia, the Journal of the Royal Society of Western Australia, and other aspects such as finances, endowments, roles, medal, housing, management and future prospects, and the early Minutes and Correspondence of the Society. A **Bibliography and Index to the Journal of the Royal Society of Western Australia** was published by Bougher & Semeniuk (1991) and updated for volumes 71-75 by Withers (1992).

As Honorary Editor of *The Journal of The Royal Society of Western Australia,* I have had the Society crest or medal reproduced for publication, and on these occasions I have wondered about their origin and meaning. However, on looking through accounts of the history of The Society I have not been able to learn anything of the history of these images. The Society was granted Royal status in 1913 and incorporated in 1937, and the first Gold (Kelvin) Medal was awarded in 1924. But, when, why and by whom were the crest and medal images produced? And what is the Seal? These questions have led me to broader issues such as of the nature of the predecessor Societies, and their Journals.

I present here a brief summary of the predecessor Societies to the Royal Society of Western Australia, a summary of their publications, and descriptions of the various crests and emblems used by the Societies.

The Western Australian Natural History Society

This Western Australian Natural History Society was founded in 1891 under the Presidency of Sir John Forrest. It was especially active in establishing a nature reserve of several thousand acres between Pinjarra, Dardalup and Bannister. Despite its early enthusiasm, its activities waned and it eventually became moribund. This Society did not survive beyond 1898, and did not publish a journal, but it provided the foundations for subsequent botanical then natural history societies in Western Australia.

The Mueller Botanic Society

In 1897, the Mueller Botanic Society was formed by a group of amateur botanists; it was inspired by and named in honour of the famous botanist Baron Ferdinand von Mueller. The first President of the Society was Sir John Forrest, with E J Bickford as Chairman.

The enthusiastic members, with the assistance of a £50 grant from the Western Australian Government, published some valuable botanical contributions in the *Journal and Proceedings of the Mueller Botanic Society* (Fig 1A). Eleven issues of Volume 1 were published between 1899 and 1903.

West Australian Natural History Society (with which is incorporated the Mueller Botanic Society)

The scope of the Mueller Botanic Society was broadened in 1903, due to widespread interest in other branches of natural history, and the title was changed to the West Australian Natural History Society with which is incorporated The Mueller Botanic Society. The first President of this society was C R P Andrews MA.

This Society published the *Journal of the West Australian Natural History Society* (Fig 1B); six issues of Volume II were published, beginning with No. 1 in May 1904, and ending with No. VI in 1909.

Natural History and Science Society of Western Australia

In 1907, several meetings of the West Australian Natural History Society lapsed for lack of a quorum and it was suggested that 'monthly' meetings only be held when there was a paper to be presented. At the Council meeting of November 1907, a subcommittee was appointed to investigate the possibility of forming a Royal Society, or affiliating with the Royal Society of South Australia, or other means. No action was taken, but in 1909 Mr A Gibb Maitland proposed that the Society be renamed the West Australian Science and Natural History Society, and at the next General Meeting the title was formerly changed to The Natural History and Science Society of Western Australia. The first President was Dr Frank Tratman.

The publications of the previous societies were continued as the *Journal of the Natural History and Science Society of Western Australia* (Fig 1C). This series commenced with Volume III No. 1 in 1910, then No. 2 in 1911, Volume "The Fourth" in 1912 and ending with Volume "The Fifth" in 1914.

The Royal Society of Western Australia

In March 1913, Mr A Gibb Maitland gave notice that he would move at the next meeting that "the time has arrived for obtaining a Royal Charter for the Society and, if granted, altering the designation to the Royal Society of Western Australia". Discussion was adjourned at the next meeting because Mr Maitland was not present, but

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P C Withers
Honorary Editor, RSWA

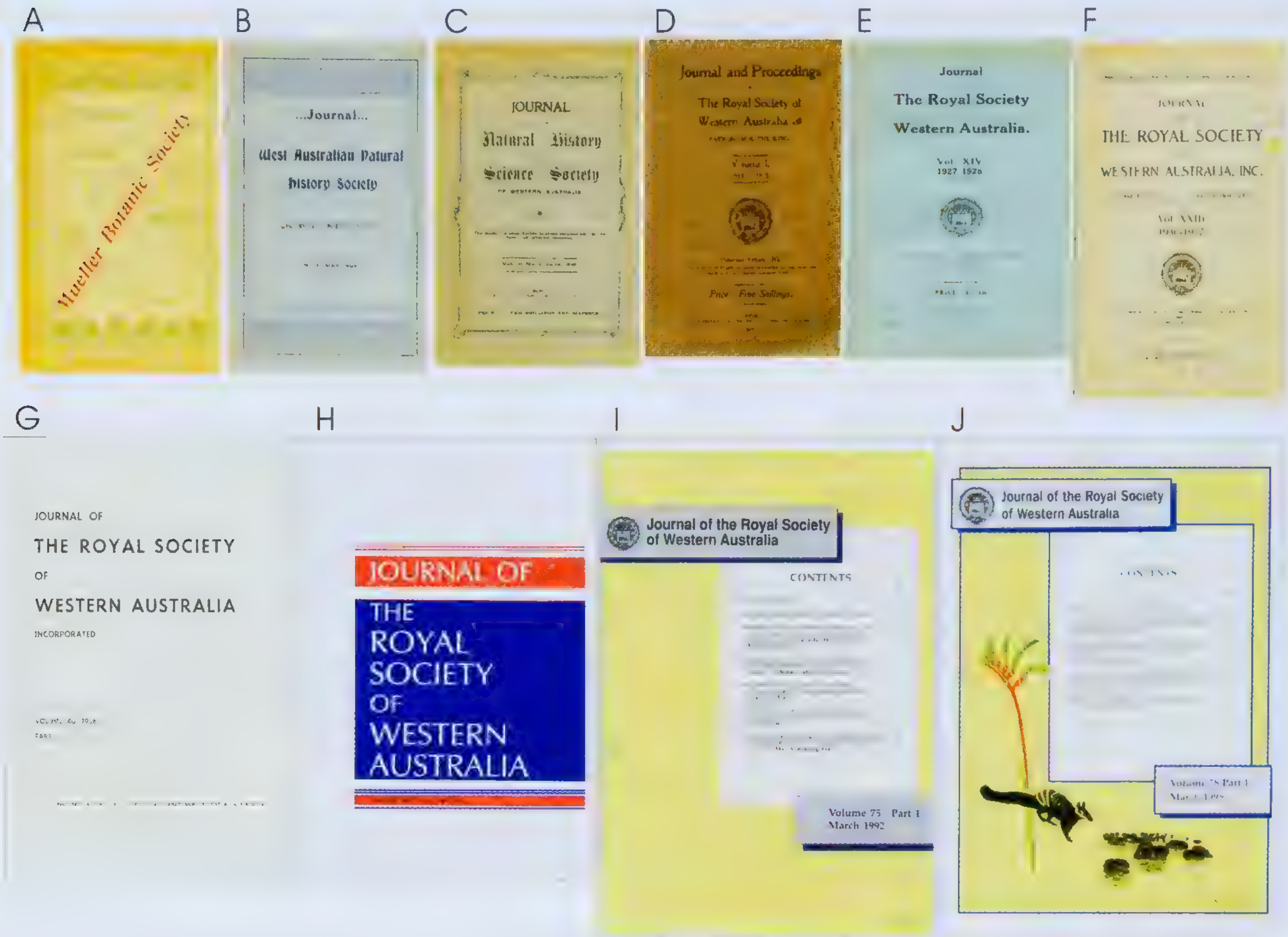

Figure 1. Covers of the various regular publications of the Royal Society of Western Australia, and its predecessor Societies.

at the May Meeting there was a preliminary discussion and it was agreed that the recent inauguration of the University (of Western Australia) meant it was an appropriate time to consider seeking a Royal Charter; in the words of the resolution of Mr Maitland, "..the time has arrived for taking the necessary steps for altering the designation to 'The Royal Society of Western Australia', and for obtaining Royal assent thereto; and that the matter be left in the hands of the Council" The resolution was carried, that "A subcommittee of Mr Maitland, Mr Grasby and the Secretary [Mr Browne] consider and report on the best manner of obtaining a Royal Charter". This subcommittee decided in June to address a memorial to His Majesty King George V and write to His Excellency the Governor Major-General Sir Harry Barron to forward the memorial to the King. Draft letters were read and recommendations carried at the Council Meeting on 10/6/1913 to proceed (copies of the letter to the Governor and the memorial to His Majesty the King are reprinted in Volume 1 pp v-vi, 1915).

Approval for the Royal Charter was received from His Majesty through The Governor in a letter dated 18/11/1913 (see Volume 1 pp vii-viii, 1915) and this was announced at the next meeting of The Society (2/12/1913). A copy of the letter conferring Royal Society status was published in The West Australian on 11/3/1914. The Society assumed its title, The Royal Society of Western Australia[+], as of 1/7/1914 (Minutes, 10/3/1914). No mention was made in any of this correspondence of The King being Patron of The Society, or of a crest for The Society. Subsequently, His Majesty was petitioned to act as Patron of The Society, which was subsequently granted (Minutes of The Society, 21/4/1914). Royal Patronage was continued by His Majesty King George VI in 1936, and by Her Majesty Queen Elizabeth II in 1952. The Society published a combined *Journal and Proceedings of the Royal Society of Western Australia* (Fig 1D) which was split at Volume XI (1924-1925) into a separate *Journal of the Royal Society of Western Australia* (Fig 1E) and Proceedings.

At its meeting on 8/6/1936, The Society decided to incorporate, and a motion was proposed and passed to this effect. With the assistance of John Nicholson MLC and the firm Nicholson & Nicholson, the process of incorporation was followed. On 13/10/36, Mr W E Shelton was named Trustee for incorporation to proceed. On 30/6/1937, all of the paperwork for incorporation had been completed and the certificate was expected early in the next financial year. The certificate was displayed at

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Footnote: The Royal Society of London was originally the "College for Improving Knowledge" but in 1661 King Charles II became a member and the College became The Royal Society. The use of "Royal" without qualification (in the British Empire) is confined to scientific bodies which share the intent of The Royal Society of London, of "improving natural knowledge". All other "Royal" societies have a qualifier *e.g.* Royal College of Surgeons, Royal Agricultural Society, Royal Zoological Society.

the 7/9/1937 meeting of The Society. Subsequent to incorporation, The Society's crest was altered to indicate the date of incorporation, which appears in Volume 33 (1936-1937) of the *Journal of the Royal Society of Western Australia* (Fig 1F).

The *Journal of The Royal Society of Western Australia* since incorporation has undergone a number of practical and cosmetic alterations. In 1955 (Volume 39), the Journal changed from roman to arabic numbering with two parts per volume, and the cover design altered to a rather plain style (Fig 1G). Then in 1956-1957 (Volume 40) the Journal was issued regularly in four parts. Colour was added to make a bolder cover style for Volume 68 in 1985 (Fig 1H). In 1991, an A4 size and restyled format was introduced to modernise the appearance of the journal, with double columns and accommodate more printed material, for the Leeuwin Current Symposium issue and the Bibliography and Index to the Journal of the Royal Society of Western Australia Supplement, then was continued for the regular issues (Fig 1I). In 1995, with the demise of Government Print, printing of the Journal was transferred to the Publications Department of the Western Museum, and a minor restyling of the cover was necessary (Fig 1J).

Crests, Medal and Seal

Perusal of *The Journal of The Royal Society of Western Australia* indicated that the original crest first appeared on the cover and front page of Volume 1, which covers the years 1914-1915 but was published in 1916. The Society received the issue from the printer on 14/11/1916. It replaced the simple but elegant flower crest (Fig 2) of The Journal of the West Australian Natural History Society (first appearing in issue No 6) then The Journal of The Natural History & Science Society of Western Australia, the last issue (Part 5) of which was published in 1914.

The Natural History and Science Society of Western Australia became The Royal Society of Western Australia by Royal decree in 1913. But what of the new Society's crest? At the September 1915 meeting of The Society, the President A. Gibb Maitland proposed that a medallion or seal be designed for The Society. At the next meeting (12/10/1915) a design for a medallion or seal was received from Mr Gibb Maitland, and it was agreed to have a block made of the design, at the expense of the Society, for use on The Society's publications and notepaper. The block was received at the next meeting (9/11/1915). Unfortunately, I could find no description of the design or block, and I presume that it was the design for the Society crest, which first appeared on the cover and front page of Volume 1 of *The Journal*. The design of the "medallion" (Fig 3), as it was referred to, was apparently not the Gold (Kelvin) Medal, which was not yet in effect. The Constitution booklet, published in 1914, did not have The Society crest.

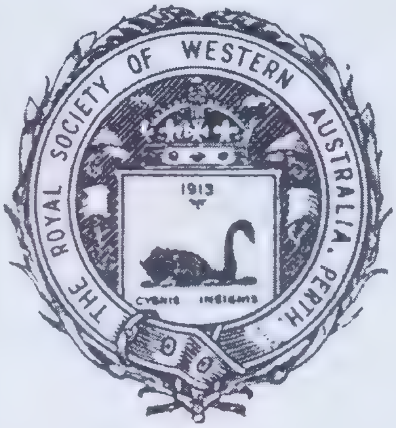
THE ROYAL SOCIETY OF WESTERN AUSTRALIA. PERTH.
1913
CYGNIS INSIGNIS

Figure 3. Crest of the Royal Society of Western Australia prior to incorporation.

At its meeting on 8/6/1936, The Society decided to incorporate, and a motion was proposed and passed to this effect. With the assistance of John Nicholson MLC and the firm Nicholson & Nicholson, the process of incorporation was followed. On 13/10/36, Mr W E Shelton was named Trustee for incorporation to proceed. On 4/3/1937, Nicholson & Nicholson requested that an impression of The Royal Society of WA seal be affixed to the incorporation documents. Soon thereafter (11/3/1937), The Society requested from Shannon's Engraving & Stamp Co a common seal with "Royal Society of W A (incorporated) Common Seal" at a cost of 17s 8d, and subsequently (23/3/1937) modified this to "The Royal Society of W A (incorporated) Common Seal" (Fig 4). On 30/6/1937, all of the paperwork for incorporation had been completed and the certificate was expected early in the next financial year. The certificate was displayed at the 7/9/1937 meeting of The Society. Subsequent to incorporation, The Societys' crest was altered to indicate

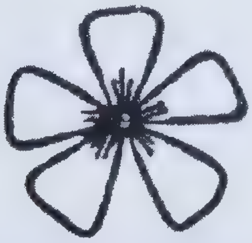

Figure 2. Emblem commonly used in the *Journal and Proceedings of the Mueller Botanic Society.*

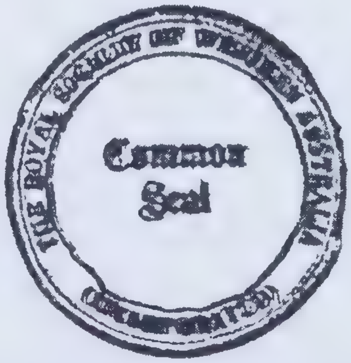
THE ROYAL SOCIETY OF WESTERN AUSTRALIA
Common
Seal
(INCORPORATED)

Figure 4. Imprint made from the "Common" or Presidential Seal of the Royal Society of Western Australia.

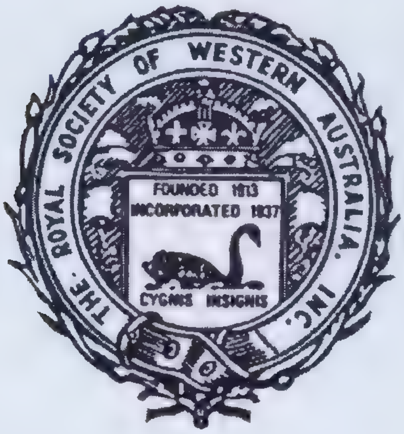

Figure 5. Crest of the Royal Society of Western Australia after incorporation.

the date of incorporation, which appears in Volume 33 (1936-1937) of *The Journal* (Fig 5).

To mark the centenary of the birth of Lord Kelvin (26/6/1824), the Royal Society of Western Australia instituted an award for outstanding work in science, the Gold Medal, now usually referred to as the Kelvin Medal. The Medal was designed by Miss Enid Isabel Allum, of 7 Richardson Street West Perth, for which she received a £5-5-0 honorarium. Miss Allum was a member of The Society, and had been Treasurer of The Society and was a member of the Social Committee. Messrs Stokes & Co, of Melbourne, was commissioned through the Royal Mint, Perth, to produce the dye for the medal, but the original drawings were lost. Miss Allum was asked to produce a second set of drawings, from which the dye (Fig 6) and two tin replicas were produced. The first medal was presented to Dr W J Hancock in 1924.

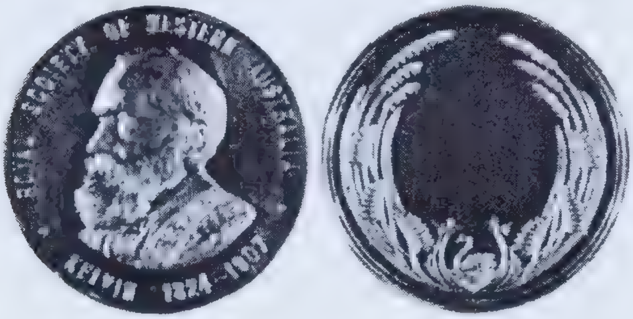

Figure 6. The Kelvin Medal of the Royal Society of Western Australia.

This modified crest has been in use by The Society until 1996, when The Council considered it opportune to modernise the layout of The Proceedings, and this included revising the crest. The new crest (Fig 7) has a stylised swan, and banksia and kangaroo paws instead of the original images (including a sheaf of papers bound in a ribbon?).

A special emblem for the Journal of the Royal Society of Western Australia was commissioned by open competition amongst members, and the design of Dr Jan Taylor was selected for use on the Journal cover (Fig 8) since Volume 75 Part 2, 1992.

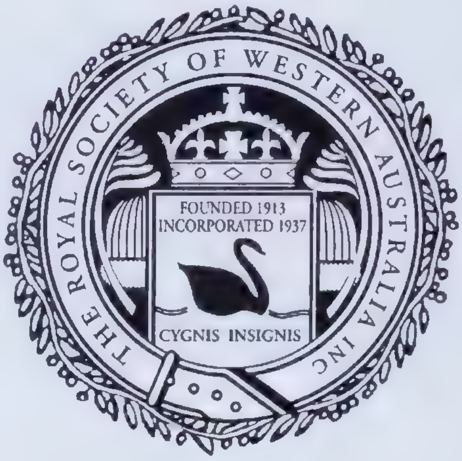

Figure 7. Revised crest of the Royal Society of Western Australia, 1997.

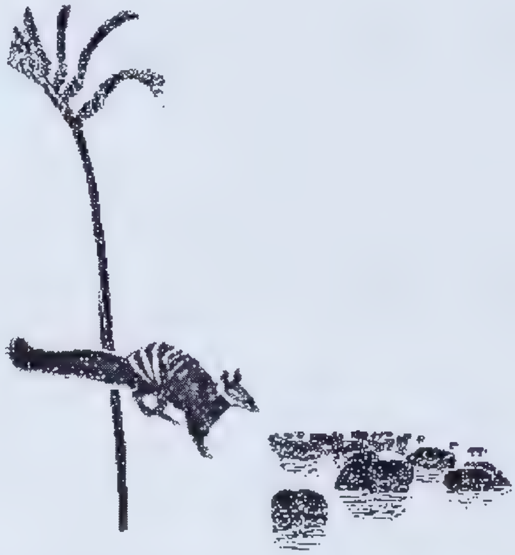

Figure 8. Emblem of the *Journal of the Royal Society of Western Australia* (by J Taylor).

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Journal of the Royal Society of Western Australia, 81: 5-12, March 1998

Officers and Councils of the Royal Society of Western Australia and previous Societies, 1897-1997

Mueller Botanic Society of Western Australia

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Librarian: J. A. Peart
Council: J. S. Battye, A. W. Milligan, D. Ross, V. F. Shotter, F. Tratman, F. M. Wilkinson

1900 *President:* E. J. Bickford
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Council: J. S. Battye, R. D. Hardey, A. W. Milligan, D. Ross, F. Tratman, F. M. Wilkinson

1900-1901 *President:* E. J. Bickford
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Other: Consulting Botanist: A. Morrison

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Other: Consulting Botanist: A. Morrison

West Australian Natural History Society (with which is incorporated the Mueller Botanic Society)

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Council: A. F. Crossman, C. P. Conigrave, E. W. Hursthouse, J. McMillan, A. W. Milligan, H. C. Prinsep
Other: Curator of Herbarium: E. W. Hursthouse

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Librarian: E. W. Hursthouse
Council: S. Blackburne, J. B. Cleland, C. P. Conigrave, T. G. Davey, E. W. Hursthouse, H. C. Prinsep, F. Tratman
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Centennial Issue: Volume 81

P C Withers
Honorary Editor, RSWA

Natural History and Science Society of Western Australia

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Council: F. G. Brown, W. Catton Grasby, H. M. Giles, T. N. Lee, E. S. Simpson

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Council: A. Gibb Maitland, L. Glauert, J. G. Hay, G. A. Pfister, C. G. Thorp

1912-1913 *President:* **C. G. Thorp**
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Librarian: A. O. Watkins
Council: A. Gibb Maitland, W. J. Hancock, A. O. Watkins, F. Tratman, A. J. Hall

Royal Society of Western Australia

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Secretary: M. A. Browne *Treasurer:* J. J. East
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1914-1915 *President:* W. J. Dakin
VicePresidents: A. Gibb Maitland, A. D. Ross
Secretaries: W. B. Alexander, M. A. Browne
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Council: F. E. Allum, C. A. Gardner, W. Catton Grasby, S. L. Kessel, A. Monygomery, G. E. Nicholls, M. A. Shelton, G. Spencer Compton

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Journal of the Royal Society of Western Australia, 81:13, March 1998

The Royal Society of Western Australia

"Kelvin" Medal Recipients

1924-1997

The Medal of The Royal Society of Western Australia was instituted in 1924 to mark the centenary of the birth of Lord Kelvin (26 June, 1825). The Royal Society Medal (originally referred to as the "Gold Medal" and then subsequently sometimes as the "Kelvin Medal' due to the association of the inaugural award with the centennial Kelvin celebration and because the medal bears in relief on its obverse side the head of Kelvin) is awarded approximately every four years for distinguished work in science connected with Western Australia.

The original dye for the medal, first struck in 1924, remains in the safe-keeping of The Society. The first three medals were struck in gold, and all subsequent medals in silver.

The first medallist of The Royal Society was Dr William J. Hancock, Government Electrical Engineer and Honorary Medical Radiographer at Perth Hospital, who in 1924 was the recipient of the Medal of The Royal Society of Western Australia, in recognition of his pioneering work in the medical application of X-rays

The most recent medallists Dr Ernest Hodgkin and Dr Arthur McComb were presented with the Medal of The Royal Society of Western Australia, in recognition of their contributions to estuarine and botanical science in Western Australia.

Recipients of the Medal of The Royal Society of Western Australia:
(reference to Journal of the Royal Society notice of medal award in parentheses)

1924	Dr W J Hancock: radiography; medical application of x-rays (10:xvii)
1929	Dr E S Simpson: mineralogy and geology of Western Australia (15:iv)
1933	Mr W M Carne: plant pathology; the bitter pit of apples (19:xi)
1937	Mr A Gibb Maitland: Pilbara survey and artesian water supplies (23:xi)
1941	Prof E de C Clarke: geology of Western Australia (27:v)
1945	Mr L Glauert: natural sciences (31:vi)
1949	Mr C A Gardner: botany, the flora of Western Australia (35:v)
1955	Dr H W Bennetts: veterinary science; live stock diseases (40:1)
1959	Prof E J Underwood: animal nutrition and husbandry (43:67)
1966	Mr C F H Jenkins: agricultural entomology and natural history (49:91)
1970	Prof R T Prider: geology; petrology and mineralogy (53:95)
1979	Prof R M Berndt: anthropology; aboriginal studies (63:29)
1979	Emer Prof B J Grieve: botany; ecophysiology and the flora of WA (63:29)
1979	Dr D L Serventy: zoology; ornithology and nature conservation
1983	Dr J S Beard: botany; vegetation classification and mapping (65:93)
1986	Prof C A Parker: soil biology
1993	Prof J R de Laeter: geophysics and geochronology (77:4)
1995	Emer Prof A R Main: zoology; ecology and nature conservation (78:89)
1997	Prof Ernest Hodgkin: estuarine studies (80:287)
1997	Prof Arthur McComb: plant growth and ecology (80:287)

Centennial Issue, Volume 81

P C Withers
Honorary Editor, RSWA

Journal of the Royal Society of Western Australia, 81:15-52, March 1998

A Complete Bibliography and Index of the Journals: 1899-1997

Journal and Proceedings of the Mueller Botanic Society
Journal of the West Australian Natural History Society
Journal of the Natural History and Science Society of Western Australia
Journal and Proceedings of the Royal Society of Western Australia
Journal of the Royal Society of Western Australia

Introduction

The objective of this Bibliography and Index is to summarise the complete publications of journals of the Royal Society of Western Australia further to the Bibliography and Index published by Bougher & Semeniuk (1991) and Withers (1992), and of journals of those Societies which were the fore-runners of the Royal Society of Western Australia, as part of this special issue commemorating 100 years of activity of these Societies in Western Australia. In addition to providing a written summary here, a searchable database containing this information concerning publications and indices will be provided on the Royal Society of Western Australia website available freely through the World-Wide-Web (http://leisuresci.fhhs.ac.cowan.edu.au/R.S.W.A./).

The Bibliography consists first of a list of publications of the Journal of the Mueller Botanic Society, the Journal and Proceedings of the West Australian Natural History Society, the Journal of the Natural History and Science Society of Western Australia, the Journal and Proceedings of the Royal Society of Western Australia, and the current Journal of the Royal Society of Western Australia. The Journals of the Mueller Botanic Society, the West Australian Natural History Society, and the Natural History and Science Society of Western Australia are consecutively numbered from one to four, and are referred to here using the Roman numerals I, II, III and IV, to distinguish them from the Journal (and Proceedings) of the Royal Society of Western Australia which restarted at Volume one, and are referred to here using the Arabic numerals 1 to 80 (even though the initial volumes of these journals themselves used Roman numerals).

The publication dates of journals are confusing for some issues, as there are sometimes two or three different dates pertaining to a single issue, with respect to publication and printing. Often there is a date on the title page of an article, and this is the primary date used here as the date of publication and for citation. There may also be a formal publication date on the cover of the issue, and this is used here as the date of publication and for citation if there is no specific date on the title page, even if it spans two years *e.g.* 1924-1925 . Finally, there may be an additional one or even two dates on the cover pertaining to the printing date. This is used as the date of publication and for citation only if none of the other dates are available. For example, Volume XXXV of the Journal of the Royal Society of Western Australia has a nominal publication date of 1948-1949 on the cover under the volume number, but has a second cover date for publication of 20th April 1951, then a further date of 1950 on the cover under the name of the Printer; the title page of articles does not have its own date. In this instance, the publication date for citation is taken to be 1948-1949.

Method of Presentation

Semeniuk (1991) listed in numeric order all of the articles of the Royal Society Journals in alphabetical order of author(s), from 1 to 819. In adding Volumes 71 to 75 to the Bibliography and Index, Withers (1992) added references 820 to 900, but of necessity starting again at A for the additional citations from 820. I have also elected to number papers in alphabetic author order from the very first paper in the Journal and Proceedings of the Mueller Botanic Society (I, 1899) to the most recent paper (Volume 80, Part 4).

The listing includes articles which are considered primary scientific articles (including Presidential Addresses) as well Prefaces and Forewords, but excludes other articles such as Annual Reports, Proceedings, Notices, Announcements, Obituaries, Errata and Corrigenda, Prefaces, Introductions *etc.* However, these other articles are retained in the database that is available through the Royal Society of Western Australia's web page.

The number of articles that are published annually by the Royal Society of Western Australia is steadily increasing, primarily because of publication of more Symposium issues.

Below are: List of Publications 1899-1997
Reference Index
Author Index
Subject Index
Locality Index
Species Index

References

Bougher A & Semeniuk V 1991 A bibliography and index to the Journal of the Royal Society of Western Australia Volumes 1-70. Journal of the Royal Society of Western Australia 74(Supplement):1-35.

Withers PC 1992 Bibliography and index to the Journal of the Royal Society of Western Australia Volumes 71-75. Journal of the Royal Society of Western Australia 75:119-126.

Centennial Issue, Volume 81

P C Withers
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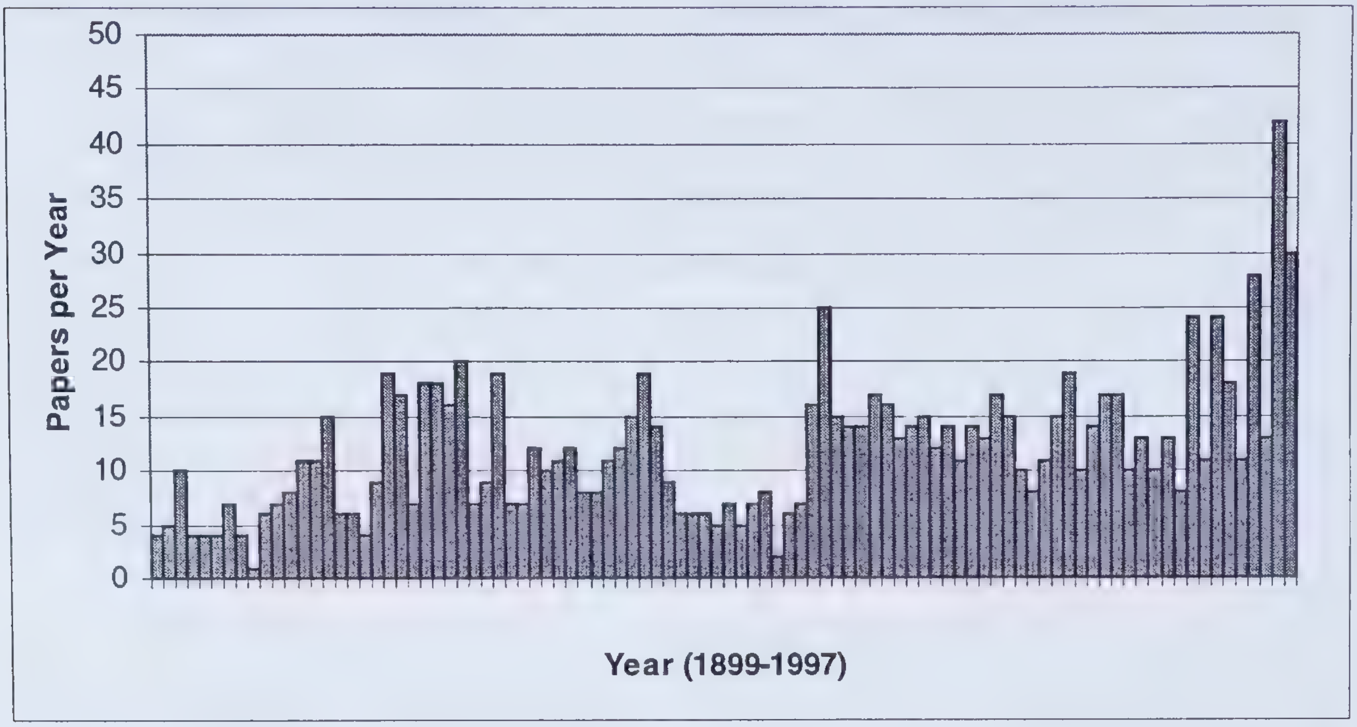

List of Publications 1899-1997

Year of publication, Volume number, Issue number, nominal date of publication [actual data of publication if different from nominal date]

Journal and Proceedings of the Mueller Botanic Society of Western Australia

1899	I	1	September, 1899
1899	I	2	October, 1899
1899	I	3	November, 1899
1899	I	4	December, 1899
1900	I	5	January, 1900
1900	I	6	May, 1900
1900	I	7	September, 1900
1900	I	8	December, 1900
1902	I	9	January/June?, 1902
1902	I	10	December, 1902
1903	I	11	April, 1903

Journal of the West Australian Natural History Society (with which is incorporated the Mueller Botanic Society)

1904	II	1	May, 1904
1905	II	2	May, 1905
1906	II	3	August, 1906
1907	II	4	November, 1907
1908	II	5	July, 1908
1909	II	6	February, 1909

Journal of the Natural History and Science Society of Western Australia

1910	III	1	June, 1910
1911	III	2	September-October, 1911
1912	IV	1	February, 1913
1914	V	1	March, 1915

Journal and Proceedings of the Royal Society of Western Australia

1914-1915	1		August, 1915 [1916]
1915-1916	2		June 1917
1916-1917	3		October-December 1918
1917-1918	4		April-May 1919
1918-1919	5		March, 1920
1919-1920	6	1	April-June, 1920 [1921]
1919-1920	6	2	January-March 1921
1920-1921	7		July-December 1921
1921-1922	8		21 December 1922
1922-1923	9	1	April 1923
1923	9	2	January 1924
1923-1924	10		November 1924

Journal of the Royal Society of Western Australia

1924-1925	11		November 1925
1925-1926	12		May-July 1927
1926-1927	13		May-June 1928
1927-1928	14		May-June 1929
1928-1929	15		March-June 1930
1929-1930	16		October 1930
1930-1931	17		August-October 1931
1931-1932	18		May-June 1933
1932-1933	19		May 1934
1933-1934	20		December 1934
1934-1935	21		December 1935-February 1936
1935-1936	22		October-November 1936
1936-1937	23		January 1938
1937-1938	24		October-November 1938
1938-1939	25		March 1940
1939-1940	26		May-June 1941
1940-1941	27		June 1943
1941-1942	28		22nd May, 1944
1943-1944	30		11th March 1946
1944-1945	31		9th April, 1948
1945-1946	32		12th July 1948
1946-1947	33		15th October 1948
1947-1948	34		6th April 1950
1948-1949	35		20th April 1951
1952	36		30th June 1952
1953	37		23rd November 1953
1954	38		19th July 1955
1955	39	1	November 1955
		2	May 1956
1956-1957	40	1	21st February 1957
		2	20th November 1957
1958	41	1	19th March 1958
		2	20th June 1958
		3	10th September 1958
		4	27th October, 1958
1959	42	1	19th March 1959
		2	2nd June 1959
		3	15th August 1959
		4	21st October 1959
1960	43	1	29th March 1960
		2	1st September 1960
		3	7th November 1960
		4	12th December 1960
1961	44	1	24th March 1961
		2	14th July 1961
		3	24th November 1961
		4	20th December 1961
1962	45	1	30th March 1962
		2	31st August 1962
		3	16th November 1962
		4	14th December 1962
1963	46	1	1st May 1963
		2	1st August 1963
		3	14th October 1963
		4	18th December 1963
1964	47	1	24th April 1964
		2	13th July 1964
		3	30th October 1964
		4	29th December 1964
1965	48	1	12th March 1965
		2	30th June 1965
		3	20th December 1965
		4	31st December 1965
1966	49	1	19th August 1966
		2	10th October 1966
		3	23rd December 1966
		4	31st December 1966
1967	50	1	25th September 1967
		2	18th December 1967
		3	19th February 1968
		4	20th May 1968
1968	51	1	5th June 1968
		2	16th August 1968
		3	10th January 1969
		4	24th February 1969
1969	52	1	30th June 1969
		2	16th September 1969
		3	11th December 1969
		4	16th April 1970
1970	53	1	17th December 1970
		2	17th December 1970
		3	8th February 1971
		4	8th February 1971
1971	54	1	18th May 1971
		2	July 1971 [28th August 1971]
		3	December 1971 [23rd February 1972]
		4	December 1971 [23rd February 1972]
1972	55	1	March [21st June 1972]
		2	July [28th November 1972]
		3	November [16th April 1973]
		4	December 1972 [16th April 1973]
1973	56	1&2	July 1973 [8th August 1973]
		3	December [14th May 1974]
		4	December 1973 [15th July 1974]
1974	57	1	May [26th August 1974]
		2	August 1974 [7th January 1975]
		3	October 1974 [7th January 1975]
		4	December 1974 [16th April 1975]
1975	58	1	May [29th August 1975]
		2	July [5th November 1975]
		3	November 1975 [9th March 1976]
		4	December 1974 [9th March 1976]
1976	59	1	May [16th June 1976]
		2	September [26th October 1976]
1977		3	February [13th April 1977]
		4	June [16th August 1977]
	60	1	September [28th October 1977]
1978		2	January [27th March 1978]
		3	February [7th April 1978]
		4	March [7th April 1978]
	61	1	September [21st July 1978]
		2	September [2nd October 1978]
1979		3	January [15th February 1979]
		4	February [7th March 1979]
	62	1-4	August 1979
1980	63	1	May [28th 1980]
		2	July [8th September 1980]
		3	September [7th November 1980]

1981		4	February [9th March 1981]
	64	1	May [25th 1981]
		2	August [21st 1981]
		3	October [9th December 1981]
1982		4	January [26th 1982]
	65	1	April [21st May 1982]
		2	June [24th 1982]
		3	August [24th 1982]
		4	December 1982 [9th February 1983]
1983	66	1&2	May [13th 1983]
	66	3	December [8th 1983]
1984	66	4	April [6th June 1984]
	67	1	April [19th December 1984]
1985	67	2	July [6th February 1986]
	67	3&4	July [16th May 1986]
	68	1	[30th June 1986]
1986		2	[29th October 1986]
		3	[29th October 1986]
		4	[22nd May 1987]
	69	1	[22nd May 1987]
1987	69	2	[16th July 1987]
	69	3	[23rd September 1987]
	69	4	[4th February 1988]
	70	1	[26th February 1988]
		2	[2nd May 1988]
1988		3	[8th November 1988]
		4	[1st December 1988]
	71	1	1988
1989		2&3	1989
		4	1989
	72	1&2	1989
1990		3	1990
		4	1990
	73	1	[July 1990]
		2	[September 1990]
1991		3	[February 1991]
		4	[August 1991]
	74		[October 1991]
	74	Supplement	[December 1991]
1992	75	1	March
		2	June
		3	September
		4	December
1993	76	1	March
		2	June
		3	September
		4	December
1994	77	1	March [March 1994]
		2	June [August 1994]
		3	September [November 1994]
		4	December [May 1995]
1995	78	1	March [June 1995]
		2	June [September 1995]
		3	September [March 1996]
		4	December [June 1996]
1996	79	1	March [November 1996]
		2	June [January 1997]
		3	September [January 1997]
		4	December [June 1997]
1997	80	1	March [August 1997]
		2	June [October 1997
		3	September [May 1998]
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Journal on Mountain Ecology = Pirineos Revista de Ecologia de Montana
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Mapa - Instituto de Geociencias, Universidade Federal do Ri Grande do Sul
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Search
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Senckenbergiana
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Treubia
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Trudy Botanicheskii Institut = Transactions of the Botanical Institute (Leningrad)
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Ukrains'kyi Botanichnyi Zhurnal = Ukranian Botanic Journal
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University of Adelaide Collected Papers
University of California Publications in Agricultural Sciences
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The Role of the Royal Society of Western Australia in the Advancement of Science

Introduction

The objective of the Royal Society of Western Australia, as stated in its Constitution, is the advancement of science in Western Australia. Throughout its nearly 100-year history, the Society has pursued this objective principally through publication of scientific papers in the *Journal of the Royal Society*, through monthly meetings, and through the convening of symposia and workshops. In more recent times, the Society has expanded its role to one of promoting science in education, and taking acquired scientific knowledge to the public arena for the wider benefit of society. Conversely, the Society has become less active in the area of formal public debate, and social and scientific commentary. Despite the changes in the role of the Society during its history, it has been holistic in its advancement of Science and has pursued or commented on a range of social, technological and scientific matters, where they interface or impinge on science.

The Society has persisted through world wars, oscillating periods of economic growth and depression, industrial revolution and environmental change, and vacillating social attitudes. During this time, the membership of the Society has expanded, and to some extent has both influenced and represented the changing social values of society.

As part of this special centenary issue of the *Journal*, we present here reflections on the Society's past and potential future contributions to science in Western Australia. We first summarise the types of traditional publications in the Journal and their implications; then we describe past activities undertaken by the Society for the advancement of science, and finally we speculate on the future role of the Society in Western Australia.

Historical Context

In any assessment or description of the role of the Society throughout its history, it would seem to be a simple matter to access the papers in and contributions to the *Journal* to determine the changing roles of the Society and the scientific directions undertaken by the Society, as determined by the influences of dominant or charismatic individuals and their motivations. No doubt, there have been individuals who through their research work, or vision, or the power of their personality have been instrumental or influential in changing the course of science in Western Australia. However, equally as important and probably very much underestimated are the individuals who have also effected change, but subtly in the background, through teaching, inspiration, and off-the-record commentaries. Their contribution must not be dismissed, but it is difficult to identify and assess such input. Thus, emphasising the achievements and influences of the former without thorough archival analyses, an activity beyond the scope of this contribution, would we believe be a historical diminishment of the latter. Further, the importance of a given paper, in terms of its influence, is difficult to assess at the time of its publication; significance is often seen only in hindsight. On the other hand, the importance of a paper in many situations cannot be fully assessed by later generations; for instance, a feature that may appear innocuous or minor to later generations, may at the time of publication of a paper have been timely and significant to the scientists of the day who did not have the advantage of hindsight.

We have opted therefore to present here an account of key activities of the Society framed simply in a historical context, rather than one based on nodal points linked to prominent individuals in the Society at any given time, or one based on external causative factors such as economics, evolving technologies, or the extant social attitudes.

Traditional Publications in the *Journal*

Scientific papers published in the *Journal of the Royal Society of Western Australia* have been wide ranging, and have advanced the scientific knowledge of Western Australia. Papers have ranged from articles summarising the state-of-the-art of a scientific endeavour, to a lifetime's work of an author *e.g.* igneous activity - Prider (1948a); or animal and plant speciation - Paterson & James (1973). Articles published have been topical *e.g.* Dakin (1915) on warfare and science, and at times controversial *e.g.* Jenkins (1948) on biological control, Burvill (1953) on soil conservation, Hatch (1959) on forest burning, Bolton and Hutchinson (1973) on European settlement, de Laeter (1979) on science and technology. The *Journal* also has provided an outlet for historical accounts of the advancement of science in the State (Jenkins 1965; Bougher & Semeniuk 1991; Withers 1992; this issue), and the development of agriculture and industry (Wood 1924; Millington 1959; Playford 1971; McPharlin & Stynes 1989; van Schagen *et al.* 1992).

The main three fields of endeavour in the Society have tended to be earth sciences, botany, and zoology. In detail, perusal of articles over the past few decades of the *Journal* reveals articles covering taxonomy, animal and plant physiology and ecology, palaeontology, mineral science, meteorites, structural geology, coastal geomorphology, stratigraphy, oceanography, archaeology, wetlands, evolution, petrology, genetics, radiometric dating, climate history and biogeography, among others.

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In the early years of the Society, when exploratory work was carried out in the State in terms of documenting the natural history of regions, there were many papers that described the biologically rich assemblages of flora and fauna *e.g.* Ashby (1929), Rayment (1930), Baird (1939), McArthur (1956), Hodgkin (1959), Koch & Majer (1980). Thus, taxonomy and documenting of Western Australian fauna and flora have featured throughout the *Journal*'s history. Similarly, the geology of the State, and particularly the Swan Region, has been described. For instance, the regional geology of Western Australia was described by Wilson (1953, 1958, 1959), and at a sub-regional level, the physiographic framework of the Swan Coastal Plain was established by Woolnough (1919), and the fundamental geology in the region around Perth was described by Prider (*e.g.* 1934, 1941, 1943, 1944, 1945, 1948b).

Papers in the *Journal* can be subdivided into four categories.

- Data papers describe some aspects of science in Western Australia – these are the most numerous of contributions.
- Presidential Addresses summarise the work carried out by an author, that provide a state-of-the-art review of the research endeavour of the author, or that provide a perspective of a scientific field by the author. For instance, Prider (1948a) described the general igneous and metamorphic geology in Western Australia as it relates to ore-formation; Glauert (1950) addressed the development of knowledge on marsupials of the State; Burvill (1953) discussed soil conservation in Western Australia, an issue which has remained topical; Beard (1989) provided a major review of the early evolution of the plant life of south-western Australia.
- Review papers provide comprehensive overviews *e.g.* the history of geology in Western Australia (Lord 1967), species diversity of south-western flora (Marchant 1973), the conservation status of *Banksia* woodlands (Hopper & Burbidge 1989).
- Symposium contributions and thematic issues; that is, papers within the context of a workshop or symposium. The symposia on "Banksia Woodlands" (Abbot 1989), the "Leeuwin Current" (Pearce & Walker 1991), "Plant Diseases" (Withers *et al.* 1994), "Design of Reserves" (Withers & Horwitz 1996), and "Granite Outcrops" (Withers & Hopper 1997) are all recent examples of such events successfully held by the Society. Publications on the general natural history of south-western Australia (McComb 1973) and Rottnest Island (Bradshaw 1983) are examples of thematic issues. In recent years, the number of papers within symposia, or special thematic issues has increased.

The publication of traditional scientific papers has contributed to general and specialist scientific knowledge in Western Australia. The implications of this are far-reaching in that the dissemination of this information has influenced government policy (Hancock 1919; Glauert 1921; Mensaros 1979; Poole 1989); provided direction for future scientific research and associated funding (Burvill 1953; Grieve 1975; Burbidge 1989); has led to the protection and further research of natural resources (Smith 1962; Main 1981; Griffin & Hopkins 1985; Hopper & Burbidge 1989; Kite & Webster 1989); has encouraged recognition of indigenous culture (Alexander 1920; Love 1930, 1931 & 1932; Bolton & Hutchinson 1973; Berndt 1974; Beard 1976), and has enhanced industrial and agricultural development in Western Australia (Alexander *et al.* 1920; Ross 1925; Carne 1927; Bennets 1935; Bowley 1941; George 1962; Lord 1967; Playford 1971; Boyd *et al.* 1976; Mulcahy 1981; Cockbain 1983; Pattiaratchi & Buchan 1991; Withers & Rosman 1996).

Many of the earlier *Journal* articles may now be viewed as having influenced the social, economic and scientific direction of Western Australia, even though at the time of publication this may not have been apparent. For instance, the development of the Western Australian agricultural industry has been assisted by early accounts of agricultural weeds (Alexander *et al.* 1920), plant diseases (Carne 1929), and livestock parasites (Bennetts 1927). Similarly, the conservation status of our flora and fauna may be attributable to early recognition of the uniqueness of the Western Australian landscape, and its inhabitants *e.g.* Fitzgerald (1917), Wood (1924), Clarke (1926) and Beard (1979). The mining industry in Western Australia also has benefited from contributions to the *Journal*. Farquharson (1922) assessed aspects of the geology of the Kalgoorlie region; Ross (1927) described the physical properties of manganese steel; Clarke (1936) addressed the issue of water supply to Kalgoorlie; Carroll (1937) described soil mineralogy; and Lord (1967) addressed the potential of mineral resources in the State. In addition, the development of many Western Australian towns and cities may have been influenced by early publications such as Saw (1919) who highlighted aspects of town planning, and Wright (1919) who discussed housing in Western Australia.

Topical Activities, Special Papers, and Commentaries

Apart from the papers published in the *Journal*, the Society has been active in investigating special problems in the State, commenting on pseudo-science, and investigating and commenting on important social, agricultural, industrial, scientific, and environmental problems. These activities have taken the form of scientific papers, reports to the Council, and letters and submissions to the Government of the day.

Of particular interest has been the periodic convening of Select Committees that investigated specific problems and then reported to the Council of the Royal Society and published their reports in the *Journal*. For instance, early in the Society's history, Select Committees and Special Papers presented information and opinions on aspects such as spiritual healing (Ross 1924), salinity (Wood 1924), and problems associated with modern currency (Allum 1922).

The Society, from time to time, has presented to relevant decision-making bodies thoughtfully considered submissions, contributions and letters on issues and problems of the day. Some of the issues in the past related to establishing flora and fauna reserves, or to protecting existing reserves from various adverse land use, and some have been related to what was considered to be scientifically adverse political decisions *e.g.* the fragmentation of the Environmental Protection Authority, and unfair dismissals of staff. Records of much of these activities are stored in the archives of the Society as letters, reports, and submissions.

The Society has endeavoured to encourage communication between scientific disciplines, and encourage community involvement in science, thereby making science more accessible. Some of the key activities, in chronological order, are briefly summarised below.

- Woodward (1907) presented a lecture on Fauna and Flora Reserves in Australasia; this topic has been an ongoing theme throughout the Society's history, with the most recent contribution being the Symposium on the Design of Reserves (Withers & Horwitz 1996).
- Dakin (1915), in a Presidential Address, commented on science and its role in warfare and national economies, and stressed that science and education should be formally recognised as a valuable resource. This commentary is as relevant now as it was 80 years ago, and yet the voice of the scientific community is often inaudible to decision makers and managers, such as politicians, urban planners, and resource managers.
- Saw (1919) published a considered article on aspects of town planning which explored and commented on important social issues of the time. Although many of the ideas contained therein would not be accepted in the light of current social values and social science paradigms, the article provided a basis for comment and debate.
- Simpson *et al.* (1919) addressed the matter of water divining, an issue important to rural south-western Australia in the early days of agricultural development, and concluded that divining rods could not be used to locate underground water flows.
- Glauert (1921) addressed at a conference the issue of 'pest' animals, with reference to both introduced animals and large populations of native species. Interestingly, the basis for classifying an organism as 'vermin' or 'protected' was determined by whether or not it reduced rabbit or insect numbers, its usefulness, and the number of complaints received. Although this approach was not entirely scientific, the current basis of pest classification is similarly based on nuisance value to humans. Of particular note is the relegation of little eagles (*Hieraaetus morphnoides*), also known as eagle-hawks, and wedge-tailed Eagles (*Aquila audax*) to the 'vermin' category, despite objection from ornithologists.
- A Special Committee of the Society, in 1923-1924, investigated and commented on the issue of Spiritual Healing (Ross *et al.* 1924), concluding that while spiritual matters can contribute to the recovery from ill health, there was no evidence of supernatural cures.
- Between 1927 and 1928, there were two Special Committees, one dealing with the problems of "Salinity in Soils", and the other dealing with "Preservation of Flora and Fauna in Reserves". Salinity was recognised as a major problem for the future, and the Special Committee investigated various aspects of the problem and submitted a final report (Wood 1927).
- A final report dealing with the preservation of flora and fauna in reserves and outlining recommendations and strategies of the Special Committee was published in the *Journal* (Shelton 1927). Increasing awareness of decline in number of various native species was its major theme, with a request for protection of the Australian bustard (*Ardeotis australis*).
- The poisonous nature of Western Australian plants was discussed in relation to agricultural stock losses (Bennetts 1935). The significance of this with regard to feral animal control was yet to be recognised.

In other matters, more in the arena of submissions, lobbying and representations, the Society became involved in issues of land management and administrative procedures where it impinged on the quality of science in Western Australia:

- In 1963 the Society was successful in instigating a survey of Aboriginal art on Depuch Island (in recognition of the importance of indigenous culture).
- In 1967, the Society persuaded the Swan River Board to enlist a biologist, and revised the Report on National Parks and Nature Reserves in Western Australia.
- In 1969, the Society was requested by the Metropolitan Regional Planning Authority to assist in assessing natural resources and heritage buildings, and to advise on matters of public interest.
- In 1970, the Society lobbied the State Government regarding the possible biological consequences of a nuclear explosion as part of a north-west harbour development, the protection of flora and fauna reserves from mining; the consequences of industrial and agricultural expansion around the Peel Inlet, Harvey Estuary, Swan Estuary and coastal waters; and the biological importance and the need to preserve the lakes and swamps of the Swan Coastal Plain.
- In 1971, the Society contributed to the Corridor Plan for Perth.
- In 1972, the Society made a submission to the Commonwealth Committee on Public Works requesting that the Garden Island naval developments be restricted to one part of the island only.
- In 1973, the Society recommended the establishment of a Research Foundation, whose aim would be to support scientific research.
- In 1974, a submission was made to the Committee of Enquiry into the National Estate, stressing the role of the Society as an unbiased and inter-disciplinary body concerned with the conservation of nature and natural reserves.

- In 1977, the increasing pressure on jarrah (*Eucalyptus marginata*) as a timber resource, was recognised through a Jarrah Forest Symposium.
- In 1981, the Society prepared a submission to the EPA regarding the System Six Report dealing with land-use and reserves in the Perth region (see Volume 64 of the *Journal*).
- In 1989, the Society made representations to the State Government over the proposed closure of the Bickley Observatory.
- In 1992, it made representations to the State Government over the splitting of the Environmental Protection Authority into two bodies.
- In 1993, it made representations to a State Government Agency over an alleged case of unfair discrimination.

In another arena, the Royal Society has made valuable contributions to the National Trust in having a permanent representative on the Council of the Trust, dealing with issues of preservation and conservation.

The Future Role of the Society - A Discussion

Over time, the role of and activities within the Society appear to have changed, from pro-active contributions on scientific and social issues, interactive involvement between members, and interactive involvement between its members and society and decision-makers, to a general overall decrease in such activities and a stronger focus on specialist research in the last 20 years. This could be attributable to several influences, some of these being: more demands on time of academics at universities, and hence less time available for activities within the Society; an increased population, hence an increased membership, and less contact between the members; more specialisation in the sciences, thus more isolation between scientists, and again, less contact time between members in areas outside their specialised field; more scientists employed in the government sector, and hence a reluctance to be publicly involved in controversial issues; higher levels of education and more insight into scientific and social complexities, and hence issues appear more difficult to address rigorously; and the increasing reluctance of decision makers to access modern knowledge and insights.

If our Society is to be viable and relevant in the future, we believe it should change from a passive Society that holds monthly meetings and produces a quarterly journal, to one that also addresses some of the issues that have resulted in the decline of its activities and possibly its influence. It should define itself and its potential future role, and become more pro-active in its scope. This may mean a more public profile, but we believe that a Society with a higher profile, prepared to speak out openly and honestly on important issues in the public arena or in the government sector, will become more respected and influential in the long term. After all, it is within our Society that a large proportion of the State's scientists reside: This is an intellectual and core-knowledge resource that could be put to effective social use. Parallels exists elsewhere in the Australian Medical Association, the Ecological Society of Australia, the Australian Academy of Science, and the Australian Marine Sciences Association; bodies that periodically release position statements relating to critical social or scientific issues, and in some cases publish the position statements in their journal (*e.g.* Saunders *et al* 1990).

Currently, the Society is redefining its role and activities, mapping out a strategy to achieve its aim of advancing science in Western Australia, and actively promoting a scientific ethos. Some of the activities in the planning stage include an annual lecture to High School students to introduce them to the Society, awarding prizes to high achievers in universities, informative public-oriented meetings, and planning more regular symposia and thematic special publications dealing with aspects of science in Western Australia.

Is this sufficient? Currently, students in Western Australia are encouraged to study science, and University courses have been expanded to specialise in almost any field of science. While organisations such as the Royal Society encourage scientific endeavour through achievement awards, the realities are that there is limited funding for employment (Majer 1997). Scientific knowledge often is overlooked in favour of political and economic gain, and political and economic forces govern funding for science (Recher, 1998). Often the consequence of this is intellectual suppression and discrimination.

In this context, has anything changed since World War I, when Dakin (1915) proffered a critical commentary directed at society for not recognising the importance of science? The Royal Society has taken an active role in the affairs of Western Australia, throughout its history, but has it been enough? Is the knowledge of scientists respected? Is this knowledge utilised to its highest potential? Herein lies one of the future challenges of the Royal Society - to foster respect and support for, and use of, scientific knowledge.

As to the future role of the Society, we believe that there should be a continuation of the ethos of the advancement of science in all its aspects, but that additionally this objective should be pursued with vision. In many regards, the global community, including Australia is in crisis, with overpopulation, environmental degradation, and social disruption (Simmons 1989; Johnson & Taylor 1989; Saunders *et al* 1990; Mannion & Bowlby 1992). Paradoxically, and perhaps to the chagrin of social scientists and to those who believe that science actually helped create the current problems, science does in part hold the key to the solution of the crisis: through identification and design of appropriate energy sources, through identification, management and reversal of environment problems, through raising the quality of human life (though not necessarily by material growth), and through education and the raising of community consciousness. While many of the critical issues are global in extent, scientists in Western Australia, and the Royal Society in particular, can be part and should be part of problem identification, design of remedial strategies, and problem resolution.

The question of whether the ethical or philosophical direction to be taken by the Society outlined above should be simply a matter of personal choice (*i.e.* at one extreme of personal indifference to matters of social and environmental importance, and at the other extreme of pro-active commentary and involvement), or one pursued in general by the Society in its advancement of science, is one that should be directed to the membership. Our own personal view is that as scientists belonging to a community who provide information and technology to the broader community, to industrialists, to decision makers, and others, and who have directly or indirectly contributed to the environmental problems, we must be accountable to broader society. Further, in recognising the issues and their potential solutions, we have a responsibility to publicly note them, and if possible to remedy or rectify them. Historically, there is a precedent for such activities, in that the Society has become involved in matters pertaining to social and environmental issues (as noted earlier). In this context, what we offer here are our considered personal views, on the future role of the Society, for discussion.

We would like to reiterate the prime objective of the Society, *to advance science in all its aspects.*

A major advantage of the Society is that it is non-specialist in nature. As scientists become increasingly specialised, and turn to specialist journals for publishing and reading, the *Journal of the Royal Society of Western Australia* provides a generalist forum for data papers and a framework for general members to keep abreast of scientific issues within other disciplines. This broad focus is one way that allows the Society to pursue its prime objective.

If one further interprets the prime objective as being the development of scientific knowledge and subsequent dissemination of this knowledge, the future role of the Society, we believe, should be linked to four important directions towards:

- continued publication of a high-quality scientific journal to disseminate original research in Western Australia, material of relevance to Western Australia, and overviews or analyses of controversial issues of great scientific moment in Western Australia;
- the appreciation of our natural and cultural heritage;
- the identification and resolution of the critical scientific, environmental and social problems of this past millennium and the next; and
- the development of individual and community potential.

Many of the issues that would be inherent in pursuing these secondary objectives have been generated by over-population, economic imperatives, under-education, and lack of knowledge - some of these clearly still can be partly resolved directly, if not indirectly by science. To survive the 21st century, human societies have to change from their commitment to population growth and its concomitant urbanisation, resource exploitation, consumption, material wealth and corporate growth, to a vision which addresses issues such as personal development, cultural development, the inherent importance of species other than *Homo sapiens*, the Rights of Nature, and the importance and significance of Heritage (Nash 1990; Robins 1992; Singer 1993; Cavalieri & Singer 1993; Flannery 1994; Recher 1997; Lines 1998; Recher 1998). Embedded in these are the legal and ethical implications of scientific knowledge and advancement, matters that are not appraised critically in our modern world.

All the matters pertinent to the secondary objectives would need to be identified as issues and then change implemented, through education, research, lobbying and political action, (scientific) cultural enrichment, and increased core-knowledge and understanding of natural science and ecological processes. Here, the Society has to expand its notion from what is the advancement of science for industrial, agricultural, medical, and general economic purposes to one that also embraces cultural and personal enrichment, and solving the critical problems.

It is suggested, therefore, that the future role of the Society should include informative public-oriented meetings, informative contributions to the media, regular non-political representations to Government, lobbying and media interaction, and adjudication in areas of scientific controversy.

To keep the Society, and science in all its aspects, in the public view, and to raise the consciousness of the public, decision makers and politicians, regarding the Society's activities and intellectual resources, it is suggested that the Society raise its profile in the community. This could be achieved in several ways, and we offer here a list of possible options:

- increasing the accessibility of the Journal to a wider scientific community through publication on the World-wide Web, and ensuring that the scientific community in Western Australia is encouraged to publish matters therein pertaining to the State, because it is the only general scientific journal specific to Western Australia;
- periodic, informative, public-oriented meetings in community settings, on matters such as salinity problems in the rural areas, or school-oriented lectures to make students aware of the existence of the Society and to raise their consciousness of the science being carried out in Western Australia;
- informative regular contributions to the media; an article in the Earth-2000 series currently active in the *West Australian* newspaper would be an example;
- regular non-political meetings with politicians or their advisors, where the Ministers (or Shadow Ministers) for the Environment, or Resources Development, or Water Resources, or Urban Planning, as well as the Chief Executive Officers of the major government agencies are invited to present their views or to take part in a mini-symposium; this would need to be done regularly as Ministers' portfolios change, so as to keep the Society in a higher profile;
- conduct conferences to foster an appreciation of the State's scientific heritage and the need for its conservation;
- lobbying, from time to time, in regard to any *ad hoc* problems, issues or controversies that arise, and submissions to relevant inquiries or Government reports; and

- have a member of Council act as a publicity officer, to regularly undertake activities to raise the profile of the Society.

As to the matter of adjudication, there have been, and will be, many situations where there are scientific controversies. These may range from the proposed mining of a National Park, to controversies regarding rehabilitation of environments, logging of perceived important forest conservation areas, contamination of soil and water, among many others. Often the controversial situation results in a stand-off with opponents unable or unwilling to resolve the issue. In such situations, where it is of benefit to the public, or for the advancement of science, the Society could offer its services as an adjudicating mediator, or offer advice from a standpoint outside the controversy. As mentioned above, within the ranks of the membership of the Society, there are numerous accomplished and specialised scientists who could provide commentary and recommendations from time to time on such critical social and scientific issues. In such cases, the Society would need to make representations to Government agencies or politicians, in advance, that this resource is available. A follow-on from this is that the Society needs to be aware of who within the ranks of the membership are willing to provide commentary, advice or specialised knowledge. The 'Register of Scientists' published by the Royal Society of Western Australia, in 1995, was an attempt to do this.

One of the underlying problems, however, that would arise for individual members of the Society as it takes a more active role as a watchdog, is that a large number of scientists are employed in the Public Sector. Graduates in science in Western Australia find employment in private organisations, in large mining or industrial companies, as consultants, in the universities, and in government organisations dealing with agriculture, minerals, forestry, conservation, fisheries, and environment. Speaking out in-house against Government activities in the mining, forestry, agricultural and urban planning sector, when employed by a Government Agency invites vilification, discrimination, discrediting, or possibly dismissal, even if the information is sound. Speaking out in a public arena amplifies the response. Discrimination, intellectual suppression, and loss of employment opportunities for intellectual dissidents is a fact of life in Australian science (Martin *et al.* 1986), and so if the Society were to take on a new role of social/scientific commentary or adjudication, it should allow for contributing individuals within the Society to avoid public identification if so desired. Essentially, for the social, legal, and employment protection of any members who contribute to this process, as well as the integrity of the Society, representations, suggestions, recommendations, or adjudications would be by the Society as a scientific body, and not as individuals within the Society.

Conclusions

During Western Australia's development, the Society consistently has contributed to scientific knowledge, disseminated information and made efforts to raise awareness in the community of the importance of science. *The Journal of the Royal Society of Western Australia* has provided an avenue for the scientific community, and has made major contributions to most facets of science.

The role of the Society may have changed over the last 100 years, but this has reflected the dynamics of social attitudes, and prioritisation of scientific pursuits. The contributions made to the advancement of science in Western Australia have been invaluable, despite these changes. Many early contributions established a framework for modern thinking on scientific matters, and it may be postulated that, in years to come, the contributions of the latter half of this century will be seen in a similar light.

The future of the Society, as well as our social and economic well-being, may depend on how well science is communicated, understood, and respected. This will only come about if the Society makes an effort to involve itself more directly in public debate on scientific and technological issues. The future role of the Society, therefore, lies in a more focused pursuit in the advancement of science to create respect for and understanding of the usefulness of science. We have outlined above our strategy to achieve this objective.

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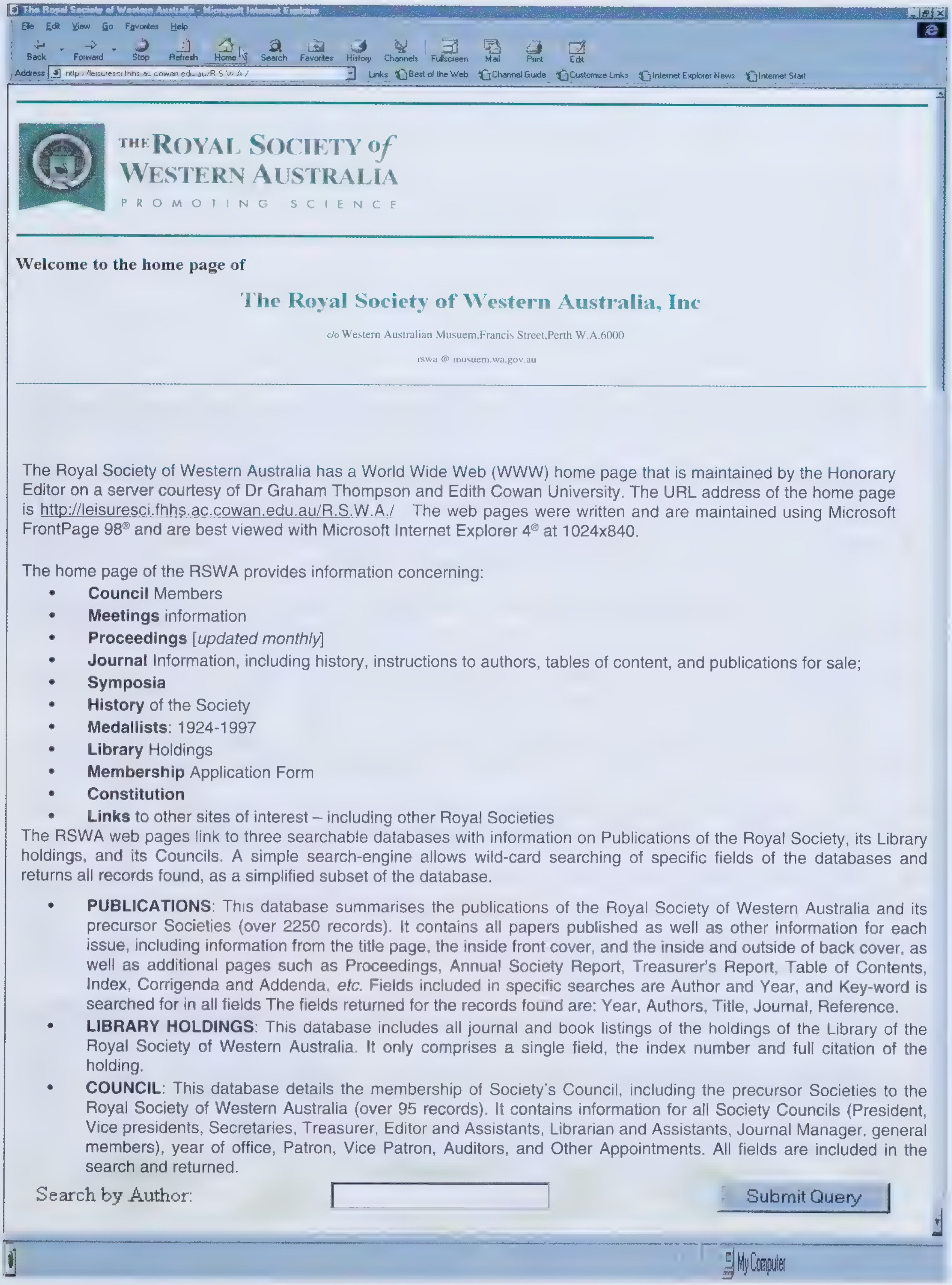
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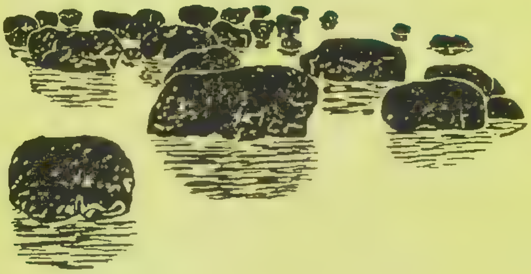

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Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences ambraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

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Passive clearing of native vegetation: livestock damage to remnant jarrah (*Eucalyptus marginata*) woodlands in Western Australia

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Abstract

In south-western Australia, areas of native forest and woodland on farmland left after agricultural clearing (remnants) have in recent times been subject to chronic disturbance by grazing livestock. We analysed adjacent grazed and ungrazed sites to assess the effects of grazing disturbance on the scleropyhll woodland community. Species richness and diversity were reduced in heavily-grazed sites and floristic dissimilarity between grazed and ungrazed sites was high. In the heavily-grazed sites, exotic species were 46% to 48% of the species recorded. Frequency and cover of native perennial species was significantly reduced in the heavily-grazed sites and in a lightly-grazed site. There was a significant increase in the frequency and cover of exotic annual grasses and herbs in the heavily grazed sites. Other life form groups such as geophytes, native perennial grasses and native annuals were not significantly affected by livestock grazing. Grazing also resulted in a significant increase in surface soil compaction and water repellency as well as concentration of soil N and P. Size-class distribution of the overstorey indicated that no recruitment had taken place for many years and, although germination of overstorey species occurred each year, no seedlings survived at the heavily grazed sites. In these sclerophyll woodlands, grazing has altered plant community structure, from a understorey dominated by perennial shrubs to one dominated by exotic annual grasses and forbs. Resilience of native perennial species is dependent on reproductive stategy, life form and morphology, life history and palatiblity. Annual exotic species are favoured by increases in soil nutrients and disturbance, reduction in competition and an ability to withstand a high level of disturbance.

Introduction

Management of native vegetation, as part of a landscape mosaic with cleared agricultural land, requires an understanding of its resilience to disturbance. Remnants of original vegetation tend to be small and isolated, and subject to many internal and external pressures including grazing (Saunders *et al.* 1991). In many parts of south-western Western Australia, clearing of remnant vegetation on farmland has been restricted by legislation for a number of years in an effort to combat land degradation such as salinization. However, although overt clearing now occurs only rarely, livestock (mainly sheep and cattle) are increasingly allowed to utilize remnant vegetation and cause varying degrees of change. While remnants may seem to be surviving well in the landscape at a superfical level, communities may be severely jeopardized in the long term, at a more detailed level.

Native eucalypt forest and woodlands with a sclerophyll shrub understorey in higher rainfall zones are not adapted to intensive herbivore grazing. Under natural conditions, these ecosystems would have been subject to sporadic grazing by sparse populations of macropods. With the introduction of domestic livestock, jarrah forest and woodlands were generally cleared and replaced with annual pasture rather than used for stock grazing. In consequence, the effects of greatly increased grazing disturbance in this environment is not well understood. For sub-alpine and semi-arid woodlands in south-eastern Australia, livestock grazing can change the vegetation structure from woodland to grassland (Chesterfield & Parsons 1985; Gibson & Kirkpatrick 1989). In other vegetation types such as Australian native grasslands, livestock grazing has resulted in an increase in unpalatable woody shrubs (Hodgkinson & Harrington 1985; Williams 1990). In plant communities that have had a long history of grazing disturbance, this disturbance is considered essential to maintaining species diversity (Carr & Turner 1959; McNaughton 1985; Noy-Meir *et al.* 1989).

Grazing affects the vegetation dynamics of remnants by influencing recruitment, mortality, dominance and age distribution of species (Wellington 1989). Direct effects of livestock grazing include the elimination of susceptible species (Wilson 1990) and the expansion of resilient species (Wimbush & Costin 1979). The need to identify susceptible (decreaser) and resilient (increaser) species is important for planning management of grazed sites (Hacker 1984). It may also be useful in ecological terms to classify species into functional groups (Hobbs 1992) based on life forms or reproductive strategies (Armstrong 1993). Maintenance of one or more species representative of each functional group may be an important strategy in restoration/management of degraded remnants (Hobbs 1992). The ability of an ecosystem to regenerate naturally may also depend on whether livestock disturbance has affected only the biotic components, such as the vegetation, or the resource base as well, such as the soil (Hobbs & Norton 1996).

Overstorey species, which in the remnants studied here are *Eucalyptus marginata* Donn ex Smith (jarrah) and *Corymbia calophylla* Lindley (marri), make up a critical functional group, through such processes as nutrient cycling, soil stabilisation and maintainence of hydrological balance, without which viability of vegetation of an area is seriously threatened. Recruitment of new trees is vital to the community's continued resilience to grazing disturbance.

A previous study (Pettit *et al.* 1995) examined the floristics of a large number of jarrah woodland remnants subjected to varying levels of livestock disturbance. This study reports on the results of a more detailed examination of 2 of these remnants, and clarifies the effects of livestock disturbance on; soil properties, survival of floristic life form groups and species with different reproductive strategies, and recruitment of overstorey species.

Methods

The study sites were located within remnants of native vegetation left after clearing for agriculture in the eastern portion of the Collie River catchment in the south west of Western Australia (33° 30' S, 116° 30' E). The landscape and soils of this area are typical of the Beraking valley landform with superfical deposits consisting mainly of sands, loams and sesquioxidic gravels up to several metres in depth on the valley slopes. These usually overlay pallid and weathered zones and granitic basement rock, with some ferruginous duricrust on the hilltops (Mulcahy & Bettenay 1972). Soil types at both locations were lateritic gravelly duplex soils with a sandy A horizon at location A and sandy loam at location B. The sites are at the eastern extent of the northern jarrah forest where jarrah and to a lesser extent marri and *Eucalyptus wandoo* Blakely (wandoo) form a woodland or open forest (Dell & Havel 1989). The understorey is dominated by perennial woody shrubs and herbs with the most abundant families being Proteaceae, Papilionaceae, Myrtaceae and Cyperaceae (Bell & Heddle 1989). The climate of the study region is Mediterranean-type with long term average annual rainfall of approxmately 650 ± 117 mm yr^{-1} of which approximately 80% falls between the months of May and October. Annual pan evaporation for the area is approximately 1600 mm and daily maximum temperature ranges from 31° C in January to 15° C in July. There are about 14 frosts per year.

Two locations were chosen from an extensive survey of remnants occurring on agricultural land in the eastern Collie River catchment (Pettit *et al.* 1995). Location A consisted of a remnant that has been heavily grazed (5 sheep ha^{-1}) for at least the past 18 years, mainly by sheep (Table 1). This was separated by a fence and road from a remnant that has had no livestock grazing for at least 10 years and any grazing which took place before this was at low stocking rates (< 0.5 sheep ha^{-1}). The second location (B) consisted of a remnant which has been heavily grazed by sheep for approximately the past seven years. This site was separated by a fence from a lightly grazed site which has been leased for grazing at low stocking rates intermittently for the past 30 years. Although grazed at low stocking rates in 1991 and 1992, this site was not grazed by sheep during 1993. A third site at Location B was situated approximately 500 m from the other two sites on the next hilltop and has never been grazed by livestock. Farmland surrounding remnants consisted of clover (*Trifolium* spp) based pasture which is regularly fertilised with superphosphate. All sites would have been subject to grazing from rabbits and native herbivores (mainly kangaroos). However this was at low densities and there was no evidence that these animals had much impact on the vegetation, at least compared with domestic livestock, at these particular sites.

At each location, two 100 m transects were established, located approximately 50 m apart and at least 50 m from

Table 1

Site characteristics for the two areas of remnant vegetation studied here.

Location	Grazing [a]	Size Ha	Surrounding land use	Surface Soil texture	% clay[b]	% coarse sand[b]	% gravel[b]	Last Fire
A	heavy (≈ 10 dse ha^{-1})	40	pasture	sand	4.3 ± 0.9	60.6 ± 2.1	71 ± 2	1974
A	past light	150	pasture, reforestation	sand	4.5 ± 1.2	61.0 ± 4.4	73 ± 4	1974
B	heavy (≈ 10 dse ha^{-1})	230	pasture, native forest	sandy loam	6.2 ± 1.9	53.4 ± 1.8	68 ± 3	≈ 1984
B	light (≈ 0.5 dse ha^{-1})	230	pasture, native forest	sandy loam	7.3 ± 2.0	53.5 ± 2.6	72 ± 4	1989
B	ungrazed	230	native forest	sandy loam	7.5 ± 2.1	58.6 ± 2.3	64 ± 5	1989

[a] dse ha^{-1} = dry sheep equivilent per hectare

[b] Mean of 10 samples of the top 10 cm of soil at each site ± standard error. Percentage gravel is for the whole soil sample. Clay and coarse sand % are for the soil sieved to < 2 mm.

the remnant boundary, to minimise edge effects. At 20 m intervals along each transect, five adjacent 1 m^2 quadrats were placed parallel to the transect with the transect line forming one side of each quadrat. This gave a total of 50 x 1 m^2 quadrats in each site. Numbers of individuals and estimated percentage cover of all species within each quadrat were recorded. For overstorey species, seedlings and saplings up to 2 m in height that formed part of the understorey were also recorded . The survey was carried out initially in August 1992 and repeated in February 1993 and August 1993 to record any seasonal changes to the vegetation and phenology of selected species. Emergence of tree seedlings (*Eucalyptus marginata* and *C. calophylla*) along the transects was recorded and seedlings tagged and survival monitored monthly over two seasons. Numbers of surviving seedlings each month were averaged over the two years. Where possible, likely cause of death of seedlings was noted. Percentage of bare ground was measured in the 1 m^2 quadrats along each transect at each site in winter and summer.

Soil samples were taken in October 1992 at each site, adjacent to the vegetation quadrats, at a depth of 0-10 cm and at 20 m intervals along each transect. Samples were sieved to < 2 mm prior to analysis. Analyses performed on all samples were total N (Kjeldahl digestion method) and P (Olsen method), organic carbon (heat of dilution method), exchangeable K (ammonium chloride method) and particle size analysis (pipette method). Descriptions of the methods of soil analyses used are given by Page *et al.* (1986) for soil chemical properties and Klute (1986) for particle size analysis. Water repellency was also measured for soil samples using the ethanol method (King 1981) where a drop of aqueous ethanol of increasing concentration (0.2 molar intervals in the range 0 - 4 M) was placed on the soil surface and the time taken for the ethanol to enter the soil was recorded. The repellence of the soil was represented by the molarity of ethanol which penetrated the soil in 10 seconds. Surface soil compaction was measured using a hand held 'pocket' penetrometer which measures soil resistance to a probe pushed into the soil to a depth of 2 cm. Measurements were taken at 2 m intervals along each transect. Deeper soil testing for compaction was unreliable at these sites because of the high lateritic gravel and boulder content of the surface soils.

Diameters at 1.3 m (DBH) of all trees (*Eucalyptus marginata* and *C. calophylla*) within 10 metres of the transect were measured to determine size class structure of the overstorey species and infer age classes.

Floristic similarity between sites was calculated using the Czekanowski coefficient (Kent & Coker 1992). For most comparisons between grazed and ungrazed sites, species were grouped into life form groups. Perennial species were also grouped according to reproductive strategy using the categories defined by Bell *et al.* (1984) *i.e.* seeders, resprouters and facultative seeder/sprouters. Importance value was also calculated for all species occurring in quadrats along the transects. This was calculated for each site as; IV (Importance Value) = relative frequency + relative abundance + relative cover. Flowering, growth and seed production of selected species representative of life form and reproductive groups were monitored monthly from winter 1992 to winter 1993.

Student t-tests and analysis of variance were used to test for differences between sites for each variable tested, and where appropriate non-parametric tests were used (Zar 1984).

Results

Effects on soil properties

There was no significant difference in proportion of clay in the top soil between sites within location A ($P = 0.825$) or B ($P = 0.687$) although there was a significant difference in the average clay content of samples between location A & B ($P = 0.03$; Table 1). The similarity in clay content of the top soil, and therefore soil texture, within a location, as well as the close proximity of sites, and similar landscape position, aspect, slope and elements of the remaining native vegetation, would suggest that comparisons between sites within locations is valid.

Soil compaction was significantly higher in the heavily grazed sites at both locations (Table 2). There was a trend toward increasing surface compaction with increasing level of grazing at Location B. Water repellency was higher in the grazed sites compared to the ungrazed sites at both locations. However water repellency of the sandy soil at the ungrazed site at location A was greater than the sandy loam sites at location B. Concentration of soil phosphorus increased with increasing level of grazing at location B while soil nitrogen concentration was significantly higher in the heavily-grazed sites at both locations. Soil potassium and organic carbon concentrations were higher in the heavily-grazed sites while carbon to nitrogen ratios were significantly higher in the heavily-grazed site at location A. The lightly-grazed site at location B had significantly higher levels of N, P and organic C than the ungrazed site.

At location A, 3% of the ground surface was bare within the quadrats at the heavily grazed site in August (winter), increasing to 25% by February (mid-summer) when annual plants would have disappeared. At the ungrazed site (location A) bare ground was 1.1% in winter and 2% in summer. At location B, there was 4% bare ground in winter at the heavily grazed site, which increased to 35% in summer, whereas at the lightly grazed site the area of bare ground was 3% in winter which increased to 4% in summer. Percentage of bare ground in the ungrazed site remained around 1.5% in summer and winter.

Species diversity

In general, species richness and diversity were lower for the grazed sites than at the ungrazed sites at each location (Table 3). Although total species richness was similar at the heavily-grazed site and the lightly-grazed site at location B, exotics represented 46% of species in the heavily-grazed site compared with 22% in the lightly-grazed site and 5% at the ungrazed site. Therefore, species richness of native flora was much less with heavy grazing. The proportion of exotic species was also high (42%) at the heavily grazed site at location A. The presence of exotics at the ungrazed site at location A (12%) may reflect past disturbance.

The Czekanowski coefficient indicated there was a high degree of floristic dissimilarity between the heavily-

Table 2

Summary of soil physical and chemical properties and how these are affected by varying levels of grazing disturbance at both locations. Significance tests performed were unpaired t-test (location A) and ANOVA (location B). Student-Newman-Kuels multiple comparison was used to compare means at location B. Values with the same letter are not significantly different ($P < 0.05$).

	Location A			Location B			
Variable Means	Heavily grazed	Ungrazed	P	Heavily grazed	Lightly grazed	Ungrazed	P
Physical							
Surface compaction (kg/cm) n=100	1.93	1.52	0.005	3.80^a	2.90^b	1.84^c	0.0001
Water Repellency n=10	2.44 (severe)	1.47 (moderate)		1.46 (moderate)	1.44 (moderate)	0.28 (very low)	
Chemical							
Total Nitrogen (%) n=10	0.27	0.19	0.009	0.22^a	0.25^a	0.12^b	0.0001
Phosphorus (ppm) n=10	101.27	73.31	0.033	87.50^a	66.80^b	27.26^c	0.0001
Potassium (ppm) n=10	148.19	116.82	0.075	238.32^a	150.51^b	91.33^b	0.0002
Organic Carbon (%) n=10	6.00	4.98	0.187	5.79^a	6.75^a	3.57^b	0.0007
C:N ratio n=10	22.27	26.73	0.0001	26.05	26.43	29.52	0.065

Table 3

Species richness, number of exotic species, species diversity (Shannon Weiner Index) and eveness (J) for the five sites at the time of the initial survey (August 1992).

	Location A		Location B		
	heavily grazed	ungrazed	heavily grazed	lightly grazed	ungrazed
Species Richness	52	67	48	46	57
Exotic species	22	8	22	10	3
Species Divesity (H)	2.91	3.07	2.48	2.82	3.17
Eveness (J)	0.72	0.73	0.63	0.70	0.77

Table 4

Czekanowski coefficient as an indicator of similarity/dissimilarity of the vegetation within and between the sites. Sites with totally similar vegetation would have a value of 1. Within site value is for the comparison between transects.

Sites	A heavily grazed	A ungrazed	B heavily grazed	B lightly grazed	B ungrazed
A heavily grazed	0.541	0.174	0.513	-	-
A ungrazed		0.569	-	0.233	0.321
B heavily grazed			0.676	0.228	0.105
B lightly grazed				0.756	0.475
B ungrazed					0.699

grazed and ungrazed sites within both locations (Table 4). By comparison, within-site floristic similarity was much higher, indicating the similarity between quadrats at each site. Due to the spatial separation of the different locations and the high level of floristic diversity in the jarrah forest (Bell & Heddle 1989), floristic similarity between the ungrazed sites at each location was low. However, similarity between heavily grazed sites at the two locations was much higher.

Changes to vegetation structure

There was a significant reduction in cover and abundance of both native shrubs and perennial herbs at the heavily-grazed sites at both locations (Table 5). In the ungrazed sites these life form groups make up 68% of the species and contribute 98% of the plant cover. At location B cover and abundance of native shrubs and perennial herbs decreased with increasing grazing pressure (Table 5). The opposite trend was seen for exotic annual grasses and forbs. Cover and abundance of native geophytes and annuals appeared not to be affected by grazing at either location. Cover and abundance of native perennial grasses was higher with heavy grazing at location A.

When perennial species were grouped according to reproductive strategy, all groups showed a significant reduction in cover and adundance in the heavily grazed sites ($P < 0.05$ in all cases). The exception was facultative seeder/sprouters at location A, with no significant difference in mean abundance between the heavily-grazed site (76) and the ungrazed site (95; $P = 0.23$). Cover of facultative seeder/sprouters at the lightly-grazed site location B (2.35%) was not significantly different from that at the ungrazed site (3.12%; $P < 0.05$). Cover of obligate seeders was also not signifcantly different in the lightly-grazed site (0.4%) from the ungrazed site (1.54%; $P < 0.05$) whereas for resprouter species cover in the lightly-grazed site (8.77%) was significantly less than at the ungrazed site (25%; $P < 0.05$).

Table 5

Comparison between different grazing intensities at location A & B of mean cover, abundance and number of species with species arranged into orgin and life form groups.

Location A

Life form*	Cover** Grazing			Abundance*** Grazing			Number of species Grazing	
	heavy	none	P†	heavy	none	P	heavy	none
Exotic annual grasses	2.22	0.06	0.012	127	12.9	0.014	10	4
Exotic annual forbs	3.2	0.13	0.024	190	8.1	0.005	12	4
Native annual forbs	0.08	0.03	0.196	38	28	0.534	3	3
Native perennial grasses	0.41	0.15	0.023	19.8	6.5	0.001	4	3
Native geophytes	0.52	0.78	0.68	89	35	0.12	13	13
Native perennial herbs	1.11	3.51	0.031	27	104	0.002	8	16
Native perennial shrubs	0.08	8.34	0.001	1	35	<0.0001	5	27
Total	7.62	13		491.8	229.5		55	67

Location B

Life form	Cover				Abundance				Number of species		
	Grazing				Grazing				Grazing		
	heavy	light	none	P††	heavy	light	none	P	heavy	light	none
Exotic annual grasses	0.85a	0.05b	0.02b	< 0.0001	118a	7b	1b	< 0.0001	11	5	2
Exotic annual forbs	2.32a	0.18b	0.06c	< 0.0001	86a	23b	1c	< 0.0001	11	5	1
Native annual forbs	0.02	0.02	0.01	0.345	9	11	8	0.803	3	3	2
Native perennial grasses	0.08	0.13	0.03	0.096	8	8	3	0.113	3	3	4
Native geophytes	0.19	0.33	0.44	0.209	20	35	26	0.157	8	9	11
Native perennial herbs	0.04c	2.37b	10.80a	< 0.0001	6c	94b	154a	< 0.0001	6	12	20
Native perennial shrubs	0.42c	7.51b	21.87a	< 0.0001	6c	34b	59a	< 0.0001	9	12	19
Total	3.90	10.54	33.20		244	201	244		48	46	57

*Native perennial grasses are all hemicryptophytes which die back to ground level during the summer; native geophytes die back to subterranean organs during summer *e.g.* Orchidacae; native perennial herbs have non-woody above ground stems or leaves that persist through summer *e.g.* many Cyperacae. **Cover measurement is the mean cover value (%) of ten 5 m x 1 m quadrats. ***Abundance measurement is mean abundance from ten 5 m x 1 m quadrats. †Significance values given using Mann-Whitney non-parametric test between sites. ††Significance values given using Kruskall-Wallis non-parametric ANOVA between sites. Student-Newman-Kuels multiple comparison (non-parametric analog) was used to separate means at location B. Values with the same letter are not significantly different ($p < 0.05$).

Table 6

Frequency, cover and abundance of the five highest ranked species according to their importance value at each site. Importance value = relative frequency + relative cover + relative abundance. eag = exotic annual grass; eaf = exotic annual forb; naf = native annual forb; ng = native geophyte; nph = native perennial herb; ps = native perennial shrub; t = tree.

Species	Frequency total (%)	Cover (%) total 50 m^2	Abundance total	Importance value
Location A				
heavily-grazed				
Hypochaeris glabra (eaf)	98	0.84	1013	42.31
Aira caryophyllea (eag)	44	1.31	716	37.47
Trifolium subterraneum (eaf)	54	1.1	156	23.94
Hypoxis glabrella (naf)	74	0.08	432	17.31
Gahnia sp (nph)	20	0.95	45	16.21
ungrazed				
Loxocarya fasciculata (nph)	84	0.88	736	34.71
Scaevola striata (nps)	74	0.96	662	32.24
Gahnia sp (nph)	66	1.47	120	18.92
Acacia pulchella (nps)	52	1.2	44	13.68
Stylidium piliferum (ng)	44	0.2	148	9.33
Location B				
heavily-grazed				
Aira caryophyllea (eag)	60	0.54	880	53.78
Hypochaeris glabra (eaf)	84	0.85	396	44.55
Trifolium subterraneum (eaf)	80	1.24	124	42.1
Medicago sp (eaf)	50	0.23	115	15.62
Vulpia myuros (eag)	52	0.15	104	13.64
lightly-grazed				
Bossiaea ornata (nps)	96	4.45	195	51.81
Lepidosperma gracile (nps)	82	0.77	704	47.73
Eucalyptus calophylla (t)	26	1.9	19	17.51
Gahnia sp (nph)	20	1.45	101	17.51
Lagenifera huegelii (ng)	62	0.13	134	13.73
ungrazed				
Bossiaea ornata (nps)	97	8.25	306	41.63
Gahnia sp (nph)	32	7.6	197	30.47
Lepidosperma gracile (nph)	78	2.28	359	26.67
Dampiera linearis (nps)	67	0.31	272	17.09
Hibbertia hypericoides (nps)	22	4.72	16	14.73

Ranking species using the importance value showed the dominance of exotic species at the heavily-grazed sites (Table 6). *Gahnia* sp (Cyperaceae), the only native perennial species to rank in the top five at either of the heavily grazed sites, is relatively common at all five sites and ranked in the top five in importance value at four of the sites. At the lightly-grazed site at location B, no exotics ranked in the top five species indicating that although exotics are present their cover and/or abundance is low compared with native species. Although the cover of *Bossiaea ornata* (Lindley) Benth at the lightly-grazed site was only half that at the ungrazed site at location B, the importance value at the lightly-grazed site is much higher. Cover and abundance of *B. ornata* was significantly less with increased grazing disturbance at location B ($P < 0.0001$). The native perennial herb *Dampiera linearis* R Br (Goodeniaceae) ranked highly at the ungrazed site at location B but only two small individuals occurred at the lightly-grazed site and it was absent from the heavily-grazed site. A similar trend was seen for the native shrub and obligate seeder *Trymalium ledifolium* Fenzel and the native perennial herb *Scaevola striata* R Br (resprouter). Cover and abundance of the native geophyte *Chamaescilla corymbosa* (R Br) F Muell ex Benth, which has a flat rosette of leaves, was not significantly different at any of the sites indicating that this species is not adversely affected by grazing.

Results of six-monthly surveys of the vegetation data along the transects showed similar trends for both locations. At all sites there was a reduction in species, cover and abundance in summer (February) as annual species and geophytes were not present. This reduction is most pronounced in the heavily-grazed sites which had the greatest proportion of annual species. In August 1993, the mean cover or number of species did not change significantly in the heavily-grazed sites or the ungrazed sites from the August 1992 survey (Fig 1). At location B in August 1993, after grazing had ceased for

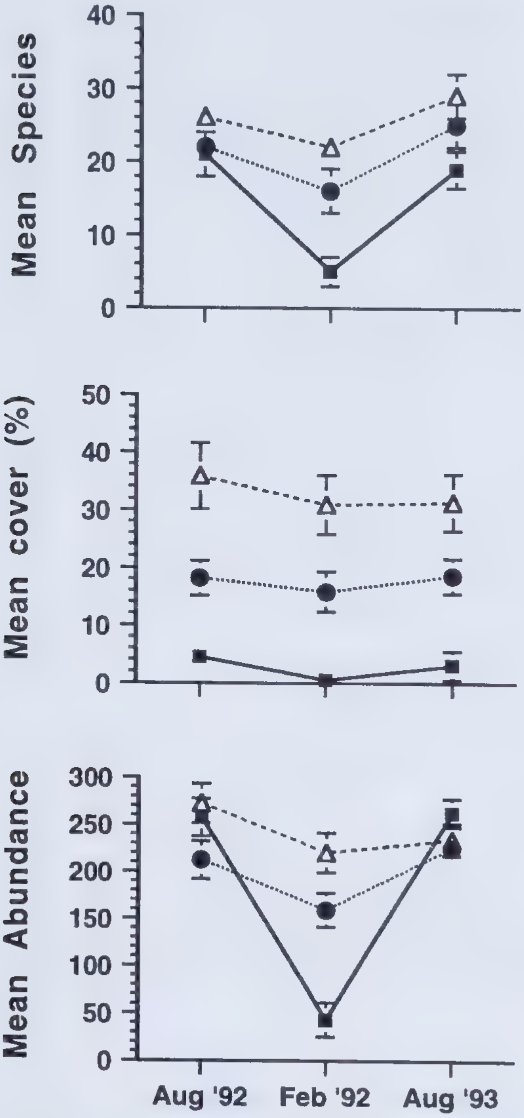

Figure 1. Mean number of species, cover and abundance (± se), along transects at each site at Location B over 12 month sampling period. Heavily grazed —■—; lightly grazed ·····●·····; ungrazed ---△---.

six months, the mean number of species was significantly greater at the lightly-grazed site than at the heavily-grazed site (P = 0.004). This separation of sites was not apparent after the initial survey in August 1992.

Phenology of selected species

The phenology of species selected as representative of different life forms and reproductive groups and response to grazing was recorded over a 12 month period (Fig 2). The annual exotic herb *Hypochaeris glabra* L flowers and sets seed almost all year round. Other annual species such as *Lagenifera huegelii* Benth and *Vulpia myuros* (L) C Gmelin had a much more restricted period of flowering and seed set which is indicative of most therophytes in the area. The growth and flowering of perennial species occurs mainly in the period of warmer temperatures and when moisture is not limiting. Flowering and seed set of *Scaevola striata* and seed set of *Dampiera linearis* was entirely within the summer period which is the period of heaviest grazing within these remnants. Others such as *Trymalium ledifolium* , and to a lesser extent *Bossiaea ornata* and *Hakea lissocarpha* flower and set seed before the onset of summer.

Size class and recruitment of overstorey species

The size class analysis of the overstorey species (*Eucalyptus marginata* and *C. calophylla*) at the two locations showed a lack of individuals in the lower size classes at the heavily-grazed sites (Fig 3). This lack of trees in smaller size classes indicates that no recruitment has taken place at these sites for many years. Conversely, individuals in the the lower size classes at the ungrazed sites indicates that some recruitment has taken place at these sites. There was emergence of tree seedlings at the heavily grazed sites as well as ungrazed sites at both Locations (Fig 4). However, a high rate of mortality occurred at the heavily-grazed sites from early summer onwards with approximately half of the deaths due to grazing. Germination of tree seed at the lightly-grazed site (location B) was lower than at the ungrazed site but mortality rates were similar to the ungrazed site with only two deaths of seedlings at each site attributable to grazing. There was also a greater proportion of *E. calophylla* seedlings at the heavily-grazed sites and at location A despite a much lower ratio of *C. calophylla* to *E. marginata* trees at all sites.

Discussion

The lack of resilience of jarrah (*Eucalyptus marginata*) woodland to heavy grazing is well illustrated by the results presented here. Grazing disturbance has affected the three major determinants of vegetation dynamics, namely, soils, vegetation composition, and structure and population dynamics and recruitment. Similar effects have been reported for grazed eucalypt woodlands of western Victoria (Wellington 1989). The present study indicates that restoration of ecosystems such as these may not be a simple matter of excluding stock, as grazing has not only affected the biotic components but also the resource base in the form of the soil (Hobbs & Norton 1996).

The high floristic dissimilarity between adjacent sites indicates the changes to the floristic structure brought about by grazing disturbance. High floristic similarity between heavily-grazed sites at the 2 locations despite the ungrazed sites having low similarity suggests that effects of grazing are overriding the usual determinants of floristic composition such as location, soil type, topography and moisture availability. The effects of light grazing are not as pronounced but are nonetheless significant. Species diversity and richness has also decreased under livestock grazing disturbance. This contrasts with environments that have had a long history of grazing disturbance and are dominated by herbaceous grasses and forbs(Milchunas & Lauenroth 1993). In other plant communities which are dominated by perennial shrubs such as heath, species diversity is also reduced (Williams & Ashton 1987).

Changes in soil characteristics under the present grazing regime benefit exotic "grazer-increaser" species while disadvantaging native species. This is characterized by increased soil compaction, water repellancy and nutrient

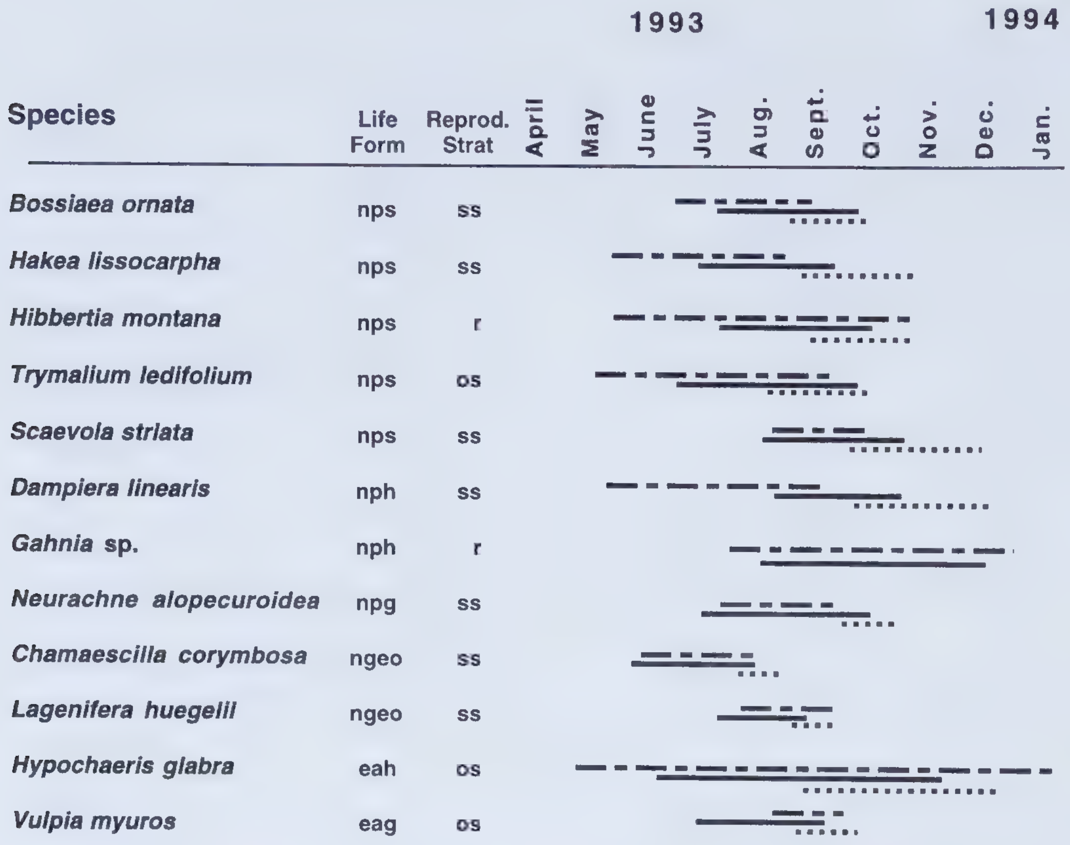

Figure 2. Phenology over 1993/1994 of selected species. Species are representative of the different life form groups and reproductive strategies of the vegetation at the 2 locations. Life form groups: nps, native perennial shrub; nph, native perennial herb; npg, native perennial grass; ngeo, native geophyte; nah, native annual herb; eah, exotic annual herb; eag, exotic annual grass. Reproductive strategy; ss, facultative seeder/sprouter; r, resprouter; os, obligate seeder. Phenology; flowering period — - — - ; growth — ; seed development ....

concentrations. Surface soil compaction, caused by trampling of the soil by livestock, may have adverse effects on moisture status and may provide a physical barrier to seedling emergence and root growth. While water infiltration in the wetter part of the year may not be affected, during summer and autumn (*i.e.* throughout the dry season) compaction may decrease infiltration of any rain which does fall and increase the risk of erosion (particularly high intensity thunderstorms) over that likely in the wet season. Annual exotic weed species which utilise only a shallow section of the topsoil through winter and spring will not be affected by decreased water infiltration in the dry season, while native perennial species establishing at the end of spring and having to survive a long dry summer/autumn may be severely affected.

The high nutrient status of grazed sites is most likely caused by drift from fertilisers applied to adjacent pasture (P) and livestock excreta and invasion of legume pasture species (N). Under fertilised regimes many native sclerophyll species develop increased shoot growth out of proportion to root growth (Specht 1963). In the dry season, the relatively under-developed root system cannot relieve the severe water stress that develops in the shoots, leading to plant death (Specht 1963).

The increase in major soil nutrients (N, P and K) and proportion of organic carbon, and the subsequent decrease in C:N ratios seen in the heavily-grazed and the lightly-grazed remnants indicate that there are dramatic changes in the nutrient cycling within remnants caused primarily by livestock disturbance. Disruption to nutrient cycling is a major cause of the deterioration of remnants (Main 1981; Hobbs 1993), especially in an environment such as jarrah woodland where the vegetation is well-adapted to nutrient poor soils (Lamont 1983). High concentrations of N and P can affect the survival of some native species (Groves & Keraitis 1976; Specht *et al.* 1977), especially the Proteaceae. Elevated concentrations of nitrogen in the leaves have also been implicated in the decline of eucalypt species as they become more attractive to insect herbivores (Landsberg 1990).

The exotic annual weeds benefit from the increased nutrient levels of the grazed sites (Panetta & Hopkins 1991) but do not have to survive the dry season. Invading exotic annual species have a competitive advantage over perennial species in highly disturbed environments. Their rapid development from germination to reproductive maturity in winter-spring enables them to grow and reproduce within the short time of relatively low grazing intensity (Miles 1979). Seed dormancy is also important in allowing these species to withstand high frequency disturbance (Grime *et al.* 1986). Invasion by exotics at the lightly grazed site was widespread although they have not yet become dominant. This may be due to there being sufficient cover of native perennial

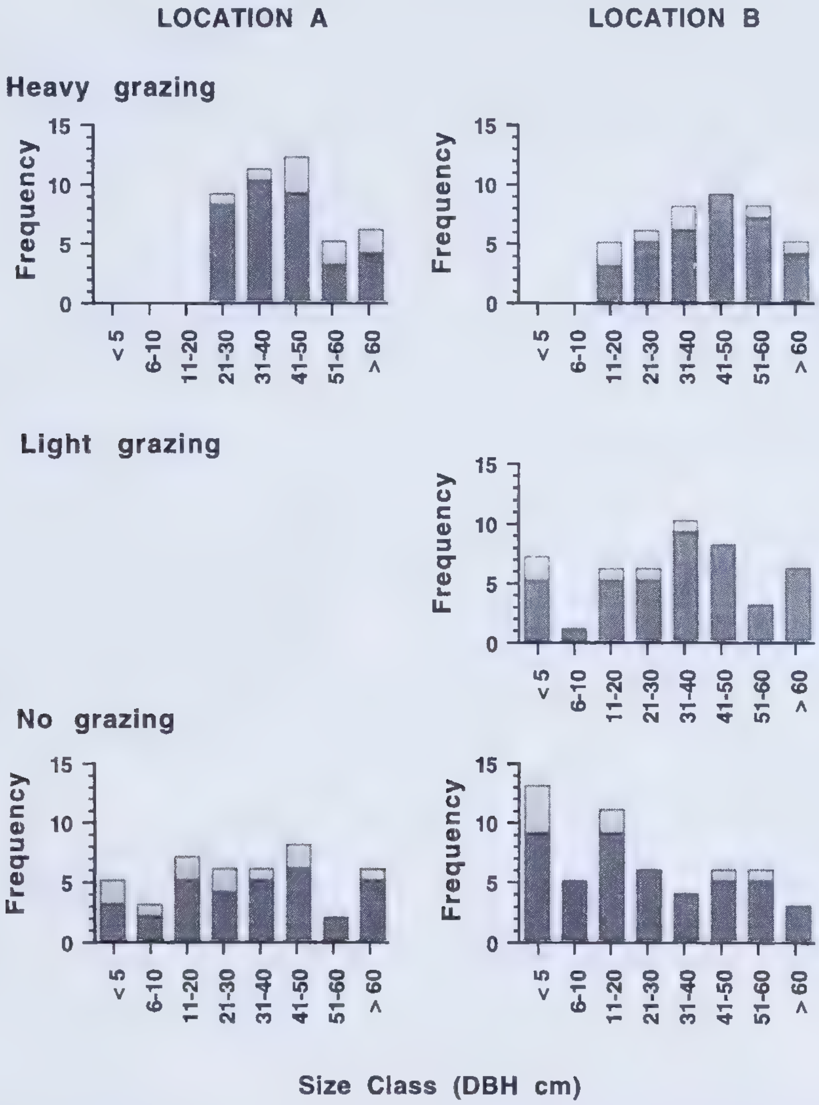

Figure 3. Size class distribution of the overstorey species measured along transects at each site at both locations. Size class measured as tree diameter overbark at breast height (1.3 m). ■ *Eucalyptus marginata*, ☐ *Corymbia calophylla*

species to prevent exotics from moving into the phase of rapid spread (Hobbs & Mooney 1993). In contrast to the situation in some arid inland areas (Hodgkinson & Harrington 1985) and in the alpine region of eastern Australia (Wimbush & Costin 1979), "woody weeds" do not appear to be a problem in jarrah forest remnants. In late winter and spring, exotic annuals are prominent while in summer and autumn cover of all understorey vegetation is much reduced in comparison with ungrazed sites.

Life form groups show clear relationships with grazing pressure. Therophytes benefit from grazing due to the increase in area of bare ground that permits establishment and reduces competition from perennial plants which have been removed. The growth phase of therophytes is at a time (winter/spring) when there is maximum herbage available, especially in the adjoining pasture, so grazing pressure in remnants is reduced. Other life form groups such as geophytes and native perennial grasses (hemicryptophytes) also benefit in this regard because they are unobtainable by exotic grazers during the time of greatest grazing stress (post spring). Although some native herbivores dig up the perennating organs of geophytes (Taylor 1992), livestock such as sheep or cattle do not seem to do this.

Among the native perennial herbs and shrubs, facultative seeder/sprouters seem less affected than obligate seeders or taxa which are strongly resprouting and have sparse seed regeneration. Facultative seeder/sprouters are thought to be the most resilient (Keeley 1986) as they are able to resprout from storage organs and regenerate freely from seed whereas populations of obligate seeders can persist only as long as seed is available in the seedbank. Resprouters need time to recover starch reserves so that they can resprout (Bowen & Pate 1993); frequent or persistant grazing therefore can exhaust reserves and eventually lead to their loss.

Perennial species which flower and/or set seed in the period of heavy grazing in summer are the most vulnerable to livestock grazing. Two such species seen here were the perennial shrubs *Scaevola striata* and *Dampiera linearis*. In a grazing simulation experiment on

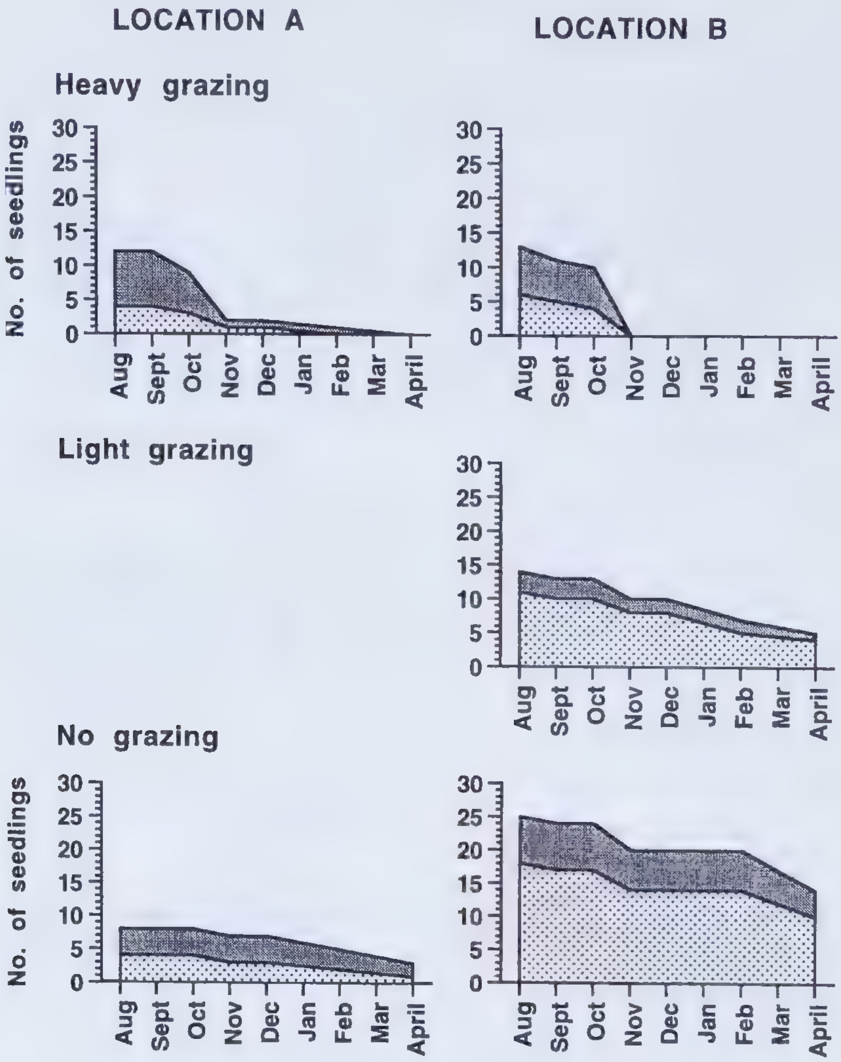

Figure 4. Occurrence and survival over a season for seedlings of overstorey species along the transects in each site at both locations. ▨ *Eucalyptus marginata*, ■ *Corymbia calophylla*

sub-alpine herbs, grazing in spring and summer reduced flowering and increased plant mortality (Leigh *et al.* 1991). Large reductions in seed production even for adapted species has been reported in grazed sub-alpine grasslands in eastern Australia (Wimbush & Costin 1979). This potential loss of seed production further reduces the vegetation's resilience to grazing pressure, especially of obligate seeders.

In the ungrazed jarrah forest there is normally a high proportion of trees in the lower size classes *i.e.* younger trees (Abbott & Loneragan 1986). In the heavily-grazed sites these younger size classes are absent, indicating that there has been little recruitment for a number of years. The disturbance of the ground under grazing provides sites for seed germination, leading to large numbers of seedlings emerging in the winter. However, the combination of grazing pressure when other herbage is sparse in summer/autumn, together with the low soil water content exacerbated by soil compaction and poor wetability, lead to virtually complete mortality of seedlings after the summer/autumn period. Seedlings of *C. calophylla* are larger and more drought tolerant than *E. marginata* seedlings, which may explain their greater abundance at the heavily-grazed sites where disturbance has created less hospitable conditions for seedling survival. The greater clay content of the surface soil at location B may also have contributed to the greater recruitment of eucalypt seedlings (particularly *E. marginata*) at the ungrazed and lightly-grazed sites. Jarrah flowers only intermittently (Abbott & Loneragan 1986) therefore seed is not always available in large numbers for regeneration. Some regenerative capacity is maintained through canopy seed store and coppice growth from lignotubers, although seed harvesting ants and livestock grazing further reduces the possibility of recruitment and regeneration.

The lack of resilience of jarrah forest remnants to heavy grazing appears to be partly the result of intensity rather than the type of grazer. Native plant species are adapted to some grazing pressure from native herbivores but they are not adapted to high intensity grazing by exotic herbivores such as sheep or cattle. Also, livestock unlike the native herbivores are hard-hoofed causing the problems of soil disturbance outlined above, especially when they are numerous. Resilience of native plant species to grazing will depend on a number of attributes. These include reproductive strategy, life form and morphology, life history and palatability.

Heavy grazing affects the 'skeleton' of the jarrah forest community (the trees and shrubs), most severely with a change in the lifeform complement of a remnant occurring progressively. Phanerophytes are replaced by mostly introduced species of therophytes, either weeds or pasture plants, and some geophytes. The long life span of the overstorey species means that visual disintegration of the woodland will take some time. However, without recruitment of these species the nature of the *Eucalyptus* spp woodland will eventually change totally. At a relatively early stage of the decline in a remnant, the structure and composition of the native community can be re-established by excluding stock (Pettit *et al.* 1995). However, under severe and prolonged grazing the lignotuber bank of resprouters and the seedbank of seed regenerators will be lost and regeneration will become very difficult.

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Flora and vegetation of the Eastern Goldfields Ranges: Part 2. Bremer Range

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Abstract

A study of the flora and plant communities of the Bremer Range greenstone belt in the spring of 1994 recorded 267 taxa. Only eight weed species were recorded but this number is likely to increase if further work is carried out in a better season. The flora list included one species gazetted as rare and new populations of five rare or poorly known taxa. Three species appear to be endemic to the Bremer Range greenstone belt, one of which was collected for the first time.

Six community types were defined from 64 sites spread across the range. The distribution of these community types appears to be primarily controlled by edaphic factors including soil water holding capacity. The floristic classification is in broad agreement with previous work but shows finer-scale patterning. None of the floristic communities or the endemic taxa are presently reserved. There has been significant impact on the vegetation of this range by mining and mineral exploration.

Introduction

The geology of ranges of the Goldfields region of Western Australia has been subject to extensive and ongoing study due to their highly prospective nature. These ranges are generally of two types, the Archaean (2500 - 3700 My old) mafic and ultramafic rocks (generally referred to as greenstone) which have undergone various degree of metamorphosis, and the banded ironstone ranges of the same age. Both major geologies are found on some ranges.

Despite the heavy exploitation of the goldfield ranges for minerals for over a hundred years, a detailed knowledge of the flora and vegetation of the region is still lacking. The aim of this series is to report on detailed floristic studies undertaken on individual ranges (Gibson *et al.* 1997). The present paper deals with the flora and vegetation of the Bremer Range greenstone belt.

Study Locality

The Bremer Range is located 170 km east of Hyden (Fig 1). The range system is 60 km long, stretching from north of Mt Day to Mt Glasse in the south. The range system is largely greenstone with small outcrops of banded ironstone, and it forms the major relief feature of the area (Gower & Bunting 1976; Hunter 1991). The topography is nonetheless subdued given the long period of erosion that this landscape has undergone. Except for the low greenstone ranges, the area consists almost entirely of gentle undulating uplands dissected by broad valleys with chains of salt lakes. These salt lake systems are the remnants of a drainage system active at an earlier time (possibly Cretaceous) of higher rainfall. Widespread laterization of the granites and greenstones is believed to have occurred during the Tertiary *i.e.* the last 65 My (Newbey 1988).

The area experiences cool winters and hot dry summers (Newbey 1988). Mean annual rainfall at Hyden (170 km west of the range) is 336 mm while at Norseman (110 km east of the range) it is 275 mm. Annual evapotranspiration is high (2150 mm at Norseman, 2230 mm at Hyden).

Beard (1976) first described the major structural formations in the area and grouped his structural units into vegetation systems. The greenstone areas of the Bremer Range, Round Top Hill, Mt Day and an unnamed hill to the north west of Mt Day form his Bremer Range vegetation system. He briefly described broom bush thickets of *Allocasuarina* on the rocky knolls, foot slopes of *Eucalyptus dundasii* and *E. longicornis*, with the lower slopes occupied by an *E. salmonophloia* association. Beard's work was followed by a regional survey of flora and fauna of the eastern goldfields (How *et al.* 1988). In the report covering the Lake Johnson - Hyden cell, Newbey & Hnatiuk (1988) described the vegetation of the Bremer Range under two main headings, banded ironstone hills and undulating greenstone plains. The banded ironstone hills were dominated by *Eucalyptus* aff *wandoo* (= *E. livida*) along with *Allocasuarina campestris*, *A. corniculata* and numerous shrubby taxa. They note that at one location on the Honman Ridge the soil was supplemented by calcareous and sub-saline material from a salt lake system. The undulating greenstone plain was described as being covered by *Eucalyptus flocktoniae* woodland with an understorey of species such as *Exocarpos aphyllus*, *Melaleuca pauperiflora*, *Acacia pachyphylla* and *A. merrallii.*

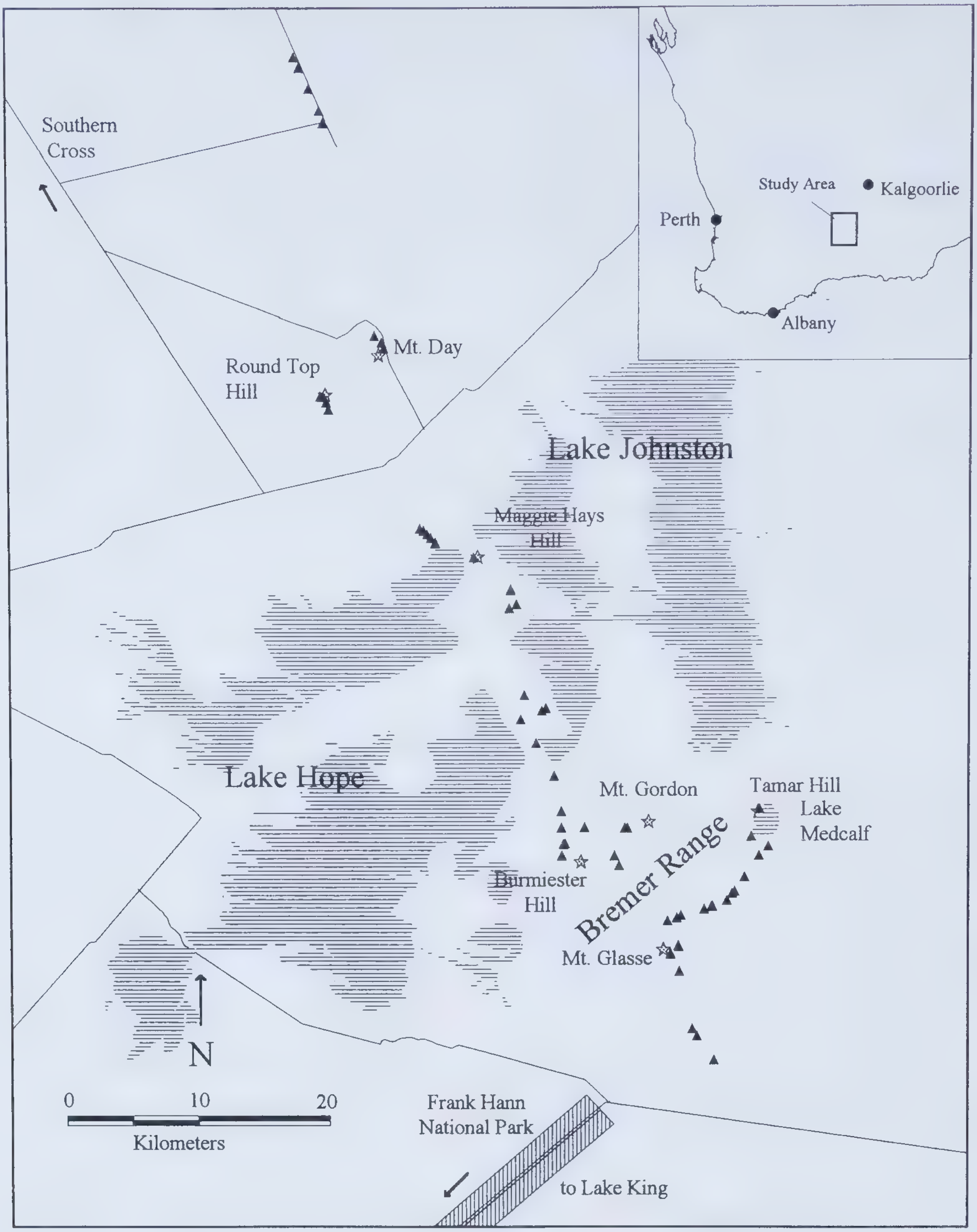

Figure 1. Location of study area. Individual sampling sites shown by solid triangles.

Both Beard's survey and the later biological survey of the eastern goldfields were undertaken to provide regional overviews. Consequently the individual greenstone ranges were not sampled extensively. Indeed, access to much of the Bremer Range was not possible at the time of these surveys. More recent work of the Bremer Range-Mt Day area has reported the occurrence of very diverse eucalypt woodlands (N Hall, CALM, and SD Hopper, Kings Park Botanic Garden, pers comm).

Methods

Sixty four 20 m x 20 m quadrats were established on the Bremer Range greenstone belt. The sites attempted to cover the major geographical, geomorphological and floristic variation. Care was taken to locate sites in the least disturbed vegetation available in the area being sampled. All sites were located in the undulating greenstone plain and banded ironstone hills units of Newbey (1988).

Within each site all vascular plants were recorded. The sites were only visited once during the spring of 1994. This was a poor year for annuals and it could be expected that the species richness of most sites would increase significantly if revisited during a good season. Data on topographical position, slope, aspect, vegetation structure and condition were collected from each site. Topographical position was scored on a subjective five point scale from ridge tops (1) to broad flats (4) to dunes beside salt lakes (5). Slope was scored on a one to three scale from flat (1) to steep (3). Aspect was recorded as one of 16 cardinal directions. Vegetation structure was recorded using Muir's (1977) classification.

All sites were permanently marked with four steel fence droppers and their positions determined using a GPS unit. Twenty four soil samples from the upper 10 cm were collected from each site. These were bulked and analysed for electrical conductivity, pH, total N, total P, percentage sand, percentage silt, percentage clay, exchangeable Na, exchangeable Ca, exchangeable Mg, and exchangeable K (Gibson *et al.* 1997).

Sites were classified according to similarities in species composition of perennial taxa. The spring of 1994 was dry with only patchy occurrence of annuals and geophytes. The classification undertaken used the Czekanowski coefficient and "unweighted pair-group mean average" fusion method (UPGMA; Sneath & Sokal 1973). Species were classified into groups according to their occurrence at the same sites by using the TWOSTEP similarity algorithm (Austin & Belbin 1982) followed by UPGMA fusion. Alternate classifications were tried using the ALOC algorithm (Belbin 1987). The resulting classifications were largely similar and only the former will be discussed in detail.

Semi-strong hybrid (SSH) ordination of the site data was undertaken to show spatial relationships between groups and to elucidate possible environmental correlates with the classification (Belbin 1991). Statistical relationships between site groups for such factors as species richness, soil parameters, slope, aspect, *etc* were tested using Kruskal-Wallis non-parametric analysis of variance and Mann Whitney U-test (Siegel 1956).

Species nomenclature follows Green (1985) and current usage at the Western Australian Herbarium. Selected voucher specimens will be lodged in the WA Herbarium.

Results

Flora

A total of 265 taxa (species, subspecies and varieties) and two hybrids were recorded from the 64 plots or the adjacent area. The most common families were Myrtaceae (63 taxa), Asteraceae (24 taxa), Mimosaceae (17 taxa), Poaceae (14 taxa), Chenopodiaceae (13 taxa), Myoporaceae (12 taxa), Proteaceae (11 taxa), Orchidaceae (10 taxa) and Rutaceae (9 taxa). Family composition was very similar to and typical of the flora of the South Western Interzone (Newbey & Hnatiuk 1988).

The most common genera were *Eucalyptus* (30 taxa), *Melaleuca* (21 taxa), *Acacia* (17 taxa), and *Eremophila* (11 taxa). Weed species were rarely encountered (8 species recorded). The 1994 spring was very poor for annual taxa except on rocky slopes where runoff collected in small depressions. The few weed records result in part from the poor season.

During the survey, two new populations of *Eucalyptus cerasiformis* were located. This species is currently listed as Declared Rare Flora (DRF; Anon 1996). New populations of a further five taxa being considered for listing as DRF were also encountered during the survey (Table 1; K Atkins, CALM, *pers comm*).

Table 1

The number of new populations found during the survey of species being considered for gazettal as Declared Rare Flora (K. Atkins, CALM pers. comm.)

Taxon	Number of new populations
Allocasuarina globosa	2
Acacia truculenta ms	3
Cryptandra polyclada	2
Eucalyptus cerasiformis	2
Eucalyptus georgei subsp *georgei*	2
Eucalyptus rhomboidea ms	11

This survey significantly extended the known range of *Eucalyptus rhomboidea* ms which was previously known only from near Mt Glasse. This species also occurs on Mt Gordon to the east and north to Round Top Hill. A new species of *Billardiera* was found on a greenstone ridge near Tamar Hill. This taxon is completely glabrous with large blue flowers and is believed to be most closely related to *B. mollis* a rare taxon found in the Ravensthorpe Ranges, 100 km to the south (E. Bennett, pers. comm.). *Eucalyptus cerasiformis, Eucalyptus rhomboidea* ms and *Billardiera* sp nov (NG&ML 1776) appear to be endemic to the Bremer Range-Mt Day greenstone belt.

The present survey recorded 72 additional taxa from the Bremer Range area (*cf* Newbey & Hnatiuk 1988), reflecting better access to the Range than was possible a decade ago. Some of these additions are also a result of improved taxonomic knowledge.

Vegetation

Some species had to be amalgamated into complexes for the floristic analysis due to difficulty of differentiating between closely related taxa without good flowering material (*e.g. Hibbertia rostellata* complex, *Melaleuca pauperiflora* complex).

One hundred and seventy perennial taxa were recorded from the 64 quadrats in the Bremer Range greenstone belt. Fifty eight taxa occurred at only one site. These singletons have little effect on the community classification and were excluded, so the final data set consisted of 112 taxa in 64 sites. Species richness ranged from 3 to 20 taxa per site, with individual taxa occurring in between 2 and 36 sites.

In this analysis, site groups are discussed at the six group level which best reflected the scale of vegetation patterning observed in the field (Fig 2). The primary division seen in the dendrogram separates the

Table 2.

Sorted two way table of the Bremer Range greenstone sites showing species occurrence by community type. Site appear as columns, species as rows.

	COMMUNITY TYPE					
	1	2	3	4	5	6
TAXA						
Species Group A						
Acacia acuminata			*		* **	
Dodonaea microzyga var *acrolobata*			* *		* *	
Allocasuarina acutivalvis					* *	
Dianella revoluta	*				**	
Dodonaea lobulata					**	
Ptilotus obovatus			*		*	
Species Group B						
Acacia duriuscula		*				**
Allocasuarina globosa						**
Eucalyptus georgei subsp *georgei*				*		*
Cheilanthes austrotenuifolia					* **	**
Eucalyptus oleosa					**	**
Eremophila decipiens		*		*		
Species Group C						
Acacia baxellii ms		*	*			
Eucalyptus cerasiformis		*			* *	
Triodia scariosa	*				*	
Eucalyptus transcontinentalis	*	* *			*	
Grevillea oncogyne	**	* *				
Species Group D						
Acacia merrallii		* *		*		
Eucalyptus cylindrocarpa		*		*		
Eucalyptus longicornis x *oleosa*		*	*			
Grevillea pectinata		* *				
Species Group E						
Acacia uncinella					** **	
Hakea scoparia					****	
Chamelaucium ciliatum					* *	
Hemigenia teretiuscula					* *	
Melaleuca cordata					**	
Baeckea crispiflora					**	
Calothamnus quadrifidus					*** *	*
Dampiera tenuicaulis					* *	
Cryptandra polyclada					* *	
Hibbertia rostellata					* **	
Pomaderris forrestiana		*			*	
Species Group F						
Allocasuarina campestris		* **			***** ** **	
Comesperma volubile		*	*	*	*** *****	
Lepidosperma sp (GJK 7000)	*	*			*** ** ** *	
Eucalyptus livida					* ***** *	
Phebalium tuberculosum	*	* * * *		* * *	** * ***	
Melaleuca uncinata	* **				*******	
Westringia cephalantha	****	*	* *	*	**** *	
Beyeria brevifolia		* * *	*		** **	
Hakea commutata		**			**	
Trymalium myrtillus		*			***	
Phebalium filifolium		*			* * *	
Allocasuarina helmsii					*	*
Thryptomene kochii					* *	
Dodonaea bursariifolia	*				***	
Rinzia sessilis					** *	
Species Group G						
Acacia camptoclada	**			**		
Acacia hystrix	* **			*		
Daviesia benthamii	***	*				
Eucalyptus eremophila	******				*	
Melaleuca acuminata	**	*				
Melaleuca lateriflora	**					
Melaleuca pentagona	**					

Table 2 (continued)

	COMMUNITY TYPE					
	1	2	3	4	5	6
Species Group H						
Acacia deficiens ms	*** *	* **				
Eucalyptus rhomboidea ms	*******	* *			* *	
Grevillea acuaria	****	* * *			*	
Wilsonia humilis	* * *	** * *				
Boronia inornata subsp *inornata*	*	* *				
Cassytha melantha	**					
Pultenaea arida	**	***	*			
Melaleuca eleuterostachya	** *				*	
Melaleuca phoidophylla ms	*	* *				
Species Group I						
Acacia erinacea	* **	* * * * **		*		*
Daviesia argillacea	* *	*** * * * ******			** *	
Eremophila clavata ms	******	* * ** *********	*	*	*	
Dodonaea stenozyga	* *	*** * ***** **** * * *	* *			
Eucalyptus flocktoniae	* *	*********** ******	** ****			
Exocarpos aphyllus	** *	**** * ** **	** **** *	*	* *	
Melaleuca pauperiflora	*******	****** **** ** * ****	******* ***	* *		
Eucalyptus salubris	*	* ** * *** * **	**			
Santalum acuminatum	***	*** *** ** *	* *****	*	* * ** *	
Microcybe multiflora var *multiflora*	* *	* * * **	*			
Acacia pachypoda	*	* * *	*	**	*	
Eucalyptus salmonophloia		* * *	**	* **	*	
Eucalyptus yilgarnensis		* *		*	*	
Acacia poliochroa		*** * ***** *	* *			
Eucalyptus dundasii		** *	**	*		
Eucalyptus tenuis		******	* *		* *	
Grevillea huegelii		* * *		* **		
Scaevola spinescens		*** *	* *	**	*	
Halgania rigida		* ***	* * *			
Eremophila alternifolia			*	**		
Species Group J						
Cassytha racemosa		**				
Eremophila densifolia subsp *pubiflora*		* **				
Eremophila psilocalyx	* *	** ** *	*			
Eucalyptus annulata		** * **	*			
Eucalyptus pileata		** ***** *	*			
Westringia rigida	**	******** *				
Eucalyptus calycogona		* * * *				
Species Group K						
Acacia truculenta ms		* *	*			
Atriplex acutibractea subsp *karoniensis*			* **			
Enchylaena tomentosa		*	**	*		
Eremophila interstans		*	*			
Atriplex vesicaria			** **	* **		
Rhagodia drummondii			* * *	* **	*	
Eremophila rugosa ms			** *			
Chenopodium curvispicatum			*******		*	
Maireana radiata			****** * *			
Sclerolaena diacantha			***********			
Zygophyllum apiculatum		* **	** ** *****	*		
Cassia nemophila		*	* *	*	*	
Cratystylis conocephala		*	* * *	* *		
Eremophila scoparia		* ** *	****	* *		
Eucalyptus longicornis		*	** *	** *		
Ptilotus holosericeus		**	* * *	***		
Alyxia buxifolia		* *** *	*		*** *	
Stenanthemum intricatum		* *	* *		*	*
Olearia muelleri	* *	**** ** * *	* *	******	* ** *	
Austrostipa elegantissima	*	** * ***** * *	** * ***	***	* * **	
Eucalyptus melanoxylon		* *		*		
Melaleuca lanceolata		**		*		

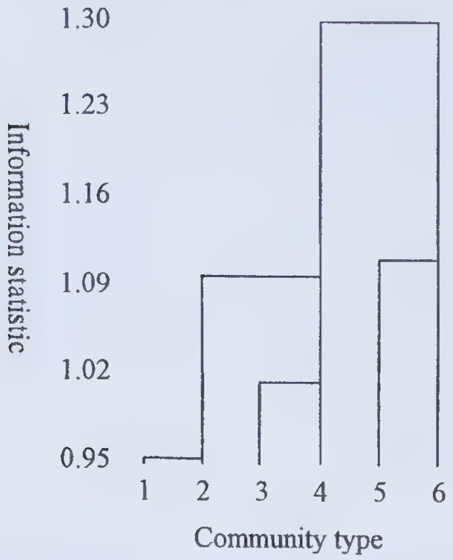

Figure 2. Dendrogram of the floristic sites from the Bremer Range area showing the six group level classification.

communities on deeper more fertile soil types (generally eucalypt woodlands, types 1 to 4) from the greenstone and lateritic ridge communities (woodlands and thickets, types 5 & 6). This division can also be clearly seen in the sorted two way table of the site and species classifications (Table 2).

- **Community type 1** generally occurs on the side slopes of low ridges and is typified by the high fidelity of species groups G and H (Table 2). This community type is typically dominated by *Eucalyptus rhomboidea* ms and *E. eremophila*. It was largely restricted to the Bremer Range proper but also flanked Round Top Hill (Fig 2). *Melaleuca* species in the *M. pauperiflora* complex were common components of the understorey in this community (and types 2 and 3). *Eremophila clavata* ms was also common in community types 1 (and type 2), while *Acacia deficiens* ms and *Grevillea acuaria* were largely restricted to community type 1.
- **Community type 2** was the typical *Eucalyptus flocktoniae* woodlands of the area. Other eucalypts co-occurring in this community included *E. salubris, E. salmonophloia, E. dundasii* and *E. tenuis*. This community type largely lacked species of groups G and H, while species group I occurred at moderate to high frequency and species group J was largely restricted to it (Table 2). It may be possible to further divide this community into a northern and a southern subgroup based on species in groups I, J, and K. Typical understorey species included *Daviesia argillacea, Dodonaea stenozyga* and *Acacia poliochroa*. This community occurred on both broad flat ridges and side slopes.
- **Community type 3** was generally dominated by *Eucalyptus flocktoniae* and /or *Eucalyptus longicornis*. This community was typical of the more saline soils as indicated by the high fidelity of many species from species group K (*e.g. Chenopodium curvispicatum, Maireana radiata, Sclerolaena diacantha* and *Zygophyllum apiculatum*). Again, species in the *M. pauperiflora* complex were common in the understorey. This community was restricted to ridges and flats adjacent to the large salt lake systems.
- **Community type 4** is similar in species composition to type 3 but has a lower frequency of the saline-tolerant species (Table 2, species group K). It was often dominated by *Eucalyptus longicornis* and /or *E. salmonophloia* but can also be dominated by *E. georgei* subsp *georgei* or *E. dundasii*. This community generally had lowest species richness of any of the eucalypt woodlands (mean 8.9 taxa /plot *cf* 14.4, 12.0 and 11.8, for types 1 to 3 respectively) and tended to occur low in the landscape. *Olearia muelleri* was the most faithful of the understorey species.
- **Community type 5** was generally dominated by either *Eucalyptus livida* woodland (on the lateritic tops) or by *Allocasuarina* thickets (on the greenstone ridges). Species typical of this community include *Allocasuarina campestris* and *Lepidosperma* sp (GJK 7000); it was widespread throughout the Bremer Range area, mostly on lateritic breakaways. Species from species groups A, B, E and F were typical of both community type 5 and 6 communities (Table 2). Mean species richness in this community was 13.2 taxa /plot.
- **Community type 6** occurred on the massive greenstone ridges with skeletal soils. Typical species from species group B included *Acacia duriuscula, Allocasuarina globosa, Eucalyptus georgei* subsp *georgei* and *Eucalyptus oleosa*. Mean species richness was to 6.5 taxa /plot. Community type 6 was only found on a greenstone ridge south east of Maggie Hays Hill.

Environmental correlates

Correlation with soil and geomorphological parameters. The soil parameters in particular showed high levels of inter-correlation (Table 3). There was significant differences between floristic group means and some geomorphological parameters (Table 4), and most soil parameters measured (Table 5). Some care needs to be taken in interpreting these results as only two quadrats were assigned to community type 6 (Figure 2 & Table 2).

The highest fertility soils were those associated with community type 3, which generally occurred on large flats adjacent to salt lakes. The saline nature of the soils can be seen from the high electrical conductivity and high exchangeable cations, in particular Na. Soils from this community type had the highest pH, total N, total P, and highest exchangeable Ca, Mg, Na, and K. Soils from community type 2 were also fertile but had significantly lower pH, total P, and total N. This community type was found on broad flats and ridge tops but did not differ significantly from community type 3 in terms of altitude, topographic or slope class (Table 4).

Community type 4 also occurred low in the landscape but had soils markedly different from community type 3, with significantly lower electrical conductivity, pH, total N, exchangeable Mg and Na, but similar total P. Soil parameters were most similar to soils of community type 2 but with a significantly lower clay content. Community type 1 tended to occur on side slopes. Its soils had low total N and P and significantly lower exchangeable Ca and K than the other lower slope woodlands.

The soils of lateritic and greenstone ridge tops (community types 5 and 6) had low total N and P, low pH and very low electrical conductivity. These community types were restricted to skeletal soils, so total available

Table 3

Matrix of Spearman rank correlation coefficients between environmental parameters. Only correlations significant at $P < 0.01$ shown ($r > 0.3245$). See methods for soil parameter codes.

	Altitude	Aspect	Ca	Clay	Conduct	K	Mg	Na	Total N	pH	Total P	Sand	Silt	Slope	Topog
Altitude	1.000														
Aspect		1.000													
Ca			1.000												
Clay				1.000											
Conduct			0.662		1.000										
K			0.712		0.649	1.000									
Mg			0.692	0.475	0.736	0.617	1.000								
Na			0.491	0.434	0.829	0.524	0.799	1.000							
Total N			0.762		0.792	0.544	0.544	0.512	1.000						
PH			0.645		0.659	0.641	0.603	0.564	0.551	1.000					
Total P	-0.339								0.497		1.000				
Sand			-0.550	-0.822	-0.460	-0.552	-0.608	-0.499		-0.414		1.000			
Silt			0.691		0.504	0.664	0.475	0.334	0.556	0.540		-0.753	1.000		
Slope		0.635												1.000	
Topog															1.000

Table 4.

Bremer Range community type means for altitude, topographic position (1-ridge top to 4-valley flat), slope class (1-flat to 3-steep), aspect (16 cardinal directions) and species richness. Non significant differences between means indicated by same superscript ($P > 0.05$, Mann-Whitney U-test).

Community Type	Altitude (m)	Topography	Slope	Aspect	Species richness
1	377.1^{a}	3.1^{ab}	1.9^{a}	4.0^{ab}	14.4^{a}
2	360.0^{ab}	3.3^{ab}	1.8^{a}	2.8^{ab}	12.0^{ab}
3	351.7^{b}	3.2^{ab}	1.8^{a}	4.9^{b}	11.8^{ac}
4	374.3^{ab}	3.9^{a}	1.7^{a}	3.7^{ab}	8.9^{bc}
5	376.7^{a}	3.0^{b}	2.0^{a}	4.3^{ab}	13.2^{a}
6	360.0^{ab}	3.0^{ab}	2.0^{a}	7.3^{b}	6.5^{b}

Table 5

Bremer Range community type means for soil parameters. Non significant differences between means indicated by same superscript ($P > 0.05$, Mann-Whitney U-test).

Community Type	Electrical Conductivity (mS m^{-1})	pH	N total (%)	P total (%)	% Sand	% Silt	% Clay	Exchangeable Ca (me %)	Exchangeable Mg (me %)	Exchangeable Na (me %)	Exchangeable K (me %)
1	19.4^{ab}	7.59^{a}	0.077^{a}	87.4^{a}	72.6^{ab}	12.5^{ab}	14.9^{ab}	7.7^{a}	4.14^{a}	0.94^{abc}	0.74^{a}
2	24.3^{a}	8.27^{b}	0.128^{b}	87.3^{a}	63.2^{a}	16.9^{b}	19.8^{a}	17.0^{b}	7.25^{bc}	1.11^{ab}	1.34^{bc}
3	41.3	8.43	0.204	143.3^{b}	67.4^{ab}	17.8^{b}	14.8^{ab}	20.1^{b}	7.58^{b}	1.61^{b}	1.63^{b}
4	20.0^{ac}	7.97^{ab}	0.119^{ab}	118.9^{ab}	71.7^{ab}	15.2^{ab}	13.1^{b}	13.8^{b}	4.76^{ac}	0.56^{ad}	1.43^{b}
5	7.2^{b}	6.43^{c}	0.097^{a}	101.0^{a}	73.7^{b}	12.0^{a}	14.4^{ab}	7.9^{a}	2.46^{d}	0.29^{e}	0.38^{d}
6	7.0^{bc}	7.15^{ac}	0.091^{ab}	80.5^{a}	68.8^{ab}	18.3^{ab}	13.0^{ab}	12.3^{ab}	3.70^{acd}	0.21^{cde}	0.57^{acd}

soil nutrients and soil moisture capacity would be very low. Because of the low number of samples of community type 6 it is not possible to characterise differences in soil parameters between the two upland community types.

Ordination results. Ordination of the sites was undertaken to show spatial relationships between groups and elucidate possible environmental correlates with the classification. The stress value was 0.23 for the three dimensional ordination. Superimposed on the ordination output (Figure 3) are best fit linear correlations of the environmental parameters measured using principal axis correlation (Belbin 1993). All parameters were range standardised prior to fitting.

The ordination shows a major gradient related to soil fertility, with community type 3 occupying the most fertile sites (Figure 3). At approximately 90 degrees to

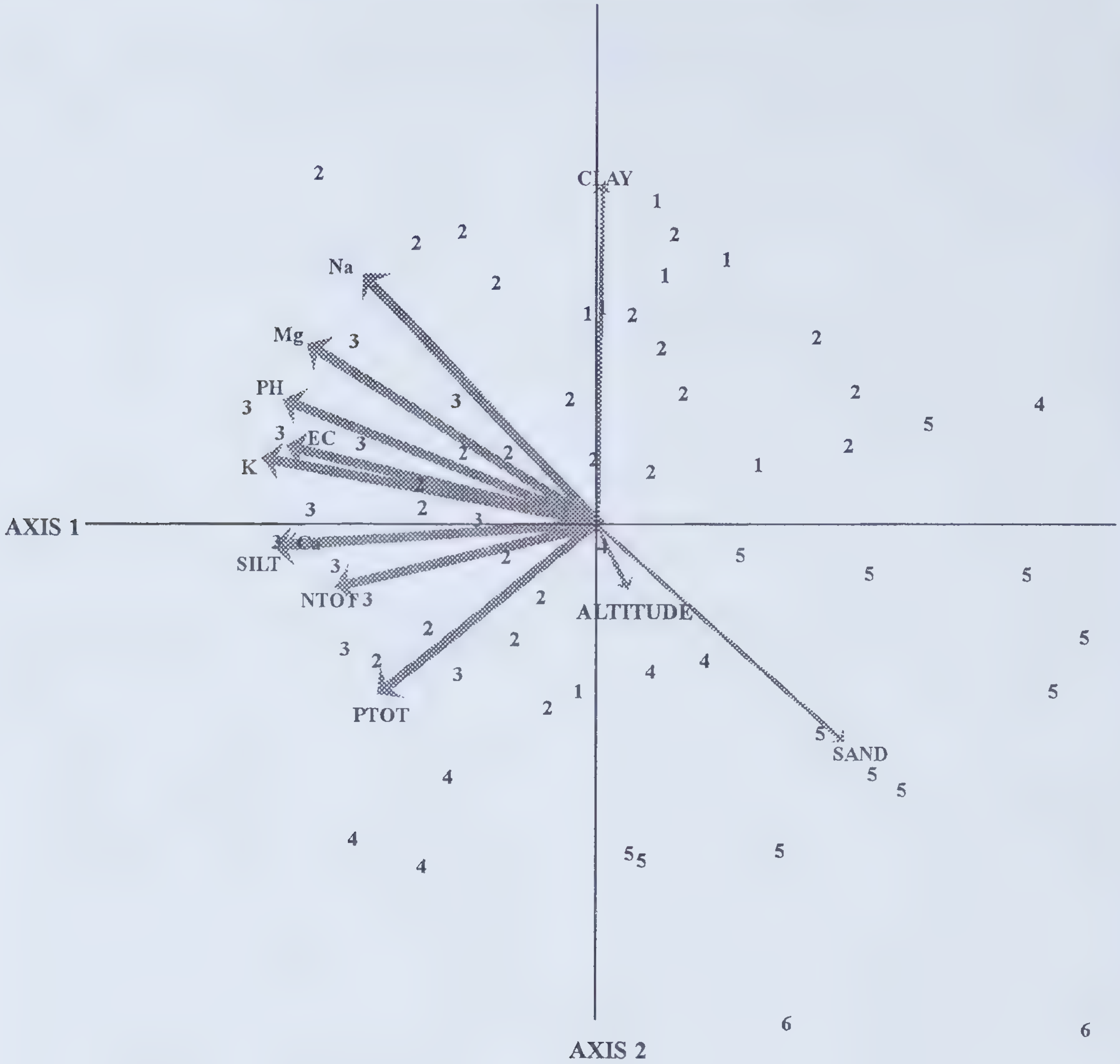

Figure 3. Ordination of Bremer Range floristic sites with numbers corresponding to community types. Arrows show the direction of the best fit linear correlation for environmental parameters. Narrow arrows are significant at $P < 0.05$, and broad arrows at $P < 0.01$, $n = 64$.

this gradient, a clear separation is seen between the ridge top communities (types 5 & 6) from the lower slope communities (Figure 3). The distribution of sites and the strong correlation with percentage sand in this direction suggests that a soil moisture availability gradient may be the secondary underlying gradient.

Discussion

Three endemic taxa have been recorded from the Bremer Range greenstone belt. This area lies within Hopper's (1979) Transitional Rainfall Zone which has undergone major fluctuations in annual rainfall during the Tertiary (last 65 My). Hopper (1979) suggested that these fluctuations have resulted in speciation centred on arid period refugia, and this may explain the number of local endemics reported from these areas. These endemics are not related to ultramafic substrates which are rare in the study area. Ultramafic areas are generally rich in endemic taxa due to the very unbalanced soil chemistry (Brooks 1987). The ultramafic areas sampled in this study showed no soil chemistry imbalance, possibly due to the very ancient nature of these formations and the subsequent long period of soil weathering.

The major differences between community types of the Bremer Range appears to be primarily related by edaphic factors with an inferred moisture holding capacity as a secondary gradient. The ridge tops of laterites and greenstones generally had much lower soil nutrient status than the colluvial deposits down slope and the alluvial and colluvial deposits of the valley bottoms. The soils with the highest nutrient status (in terms of N and P) had the highest electrical conductivity and the highest exchangeable Na and Ca. They also occurred low in the landscape and their higher salinity probably reflects down slope leaching over most of the Tertiary.

The previous work undertaken in the study area described broad regional vegetation patterns (Beard 1976; Newbey & Hnatiuk 1988). Our results are generally consistent with those descriptions but show finer scale patterning. Some of the vegetation units described above (community types 1 - 4) are also described as occurring on the Broad Valley unit of Newbey & Hnatiuk (1988). Our study supports Beard's concepts of the Bremer Range Vegetation System (Beard 1976). One of our community types showed some north-south subdivision, another was very localised and the remaining four were spread throughout the greenstone belt.

None of Beard's (1976) Bremer Range vegetation system currently occurs in any conservation reserve; similarly the three endemic species on Bremer Range are completely unreserved. Significant conservation reserves have been proposed for the area around Mt Day and the Bremer Range proper (Anon 1992), however these are yet to be acted upon. The current proposals would adequately conserve both the flora and communities of the Range except for community type 6 which is only know from greenstone ridge south east of Maggie Hays Hill.

Both past and present mineral exploration activity are having a significant impact on the vegetation of this area, especially within small geomorphological units. We saw little evidence of rehabilitation of exploration tracks, costines or drill sites. There is an urgent need to improve environment management of mineral exploration on Vacant Crown Lands.

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Appendix 1

Flora list for the Bremer Range greenstone belt (* indicated introduced species). Taxa with collection numbers are lodged in the Western Australian Herbarium.

- Adiantaceae
  - *Cheilanthes austrotenuifolia*
- Aizoaceae
  - *Carpobrotus* sp
- Amaranthaceae
  - *Ptilotus holosericeus*
  - *Ptilotus obovatus*
- Anthericaceae
  - *Borya constricta*
  - *Thysanotus patersonii*
- Apiaceae
  - *Daucus glochidiatus*
  - *Homalosciadium homalocarpum*
  - *Hydrocotyle pilifera var glabrata*
  - *Hydrocotyle rugulosa*
  - *Platysace maxwellii*
  - *Trachymene cyanopetala*
  - *Trachymene ornata*
- Apocynaceae
  - *Alyxia buxifolia*
- Asteraceae
  - *Actinobole uliginosum*
  - *Asteridea athrixioides*
  - *Asteridea pulverulenta*
  - *Blennospora drummondii*
  - *Brachyscome iberidifolia*
  - *Calotis hispidula*
  - *Cratystylis conocephala*
  - *Hyalosperma demissum*
  - * *Hypochaeris glabra*
  - *Isoetopsis graminifolia*
  - *Millotia tenuifolia*
  - *Olearia dampieri* subsp *eremicola* ms
  - *Olearia muelleri*
  - *Podolepis capillaris*
  - *Podolepis lessonii*
  - *Rhodanthe laevis*
  - *Rhodanthe manglesii*
  - *Rhodanthe oppositifolia* subsp *oppositifolia*
  - *Rhodanthe pygmaea*
  - *Senecio glossanthus*
  - *Senecio* sp (NG & ML 2323)
  - * *Sonchus oleraceus*
  - * *Ursinia anthemoides*
  - *Waitzia acuminata*
- Boraginaceae
  - *Halgania rigida*
  - *Halgania viscosa*
  - *Omphalolappula concava*
- Brassicaceae
  - *Stenopetalum robustum*
- Caesalpiniaceae
  - *Cassia nemophila*
- Campanulaceae
  - *Wahlenbergia gracilenta*
- Caryophyllaceae
  - *Stellaria filiformis*
- Casuarinaceae
  - *Allocasuarina acutivalvis*
  - *Allocasuarina campestris*
  - *Allocasuarina corniculata*
  - *Allocasuarina globosa*
  - *Allocasuarina helmsii*
- Celastraceae
  - *Psammomoya choretroides*
- Chenopodiaceae
  - *Atriplex acutibractea* subsp *karoniensis*
  - *Atriplex vesicaria*
  - *Chenopodium curvispicatum*
  - *Enchylaena tomentosa*
  - *Halosarcia entrichoma*
  - *Maireana erioclada*
  - *Maireana radiata*
  - *Maireana trichoptera*
  - *Rhagodia drummondii*
  - *Sclerolaena diacantha*
  - *Sclerolaena drummondii*
  - *Sclerolaena eurotioides*
  - *Threlkeldia diffusa*
- Convolvulaceae
  - *Wilsonia humilis*
- Crassulaceae
  - *Crassula colorata*
- Cupressaceae
  - *Callitris glaucophylla*
- Cyperaceae
  - *Gahnia lanigera*
  - *Lepidosperma* sp (GJK 7000)
  - *Lepidosperma* sp (KRN 7815)
  - *Lepidosperma* sp (NG & ML 2075)
  - *Schoenus nanus*
- Dilleniaceae
  - *Hibbertia rostellata* complex
- Droseraceae
  - *Drosera macrantha* subsp *macrantha*
- Epacridaceae
  - *Astroloma serratifolium*
  - *Coleanthera myrtoides*
  - *Leucopogon cuneifolius*
  - *Styphelia pulchella*
- Euphorbiaceae
  - *Beyeria brevifolia*
  - *Ricinocarpos stylosus*
- Fabaceae
  - *Daviesia argillacea*
  - *Daviesia benthamii*
  - *Gastrolobium crassifolium*
  - *Mirbelia* sp (NG & ML 1881)
  - *Pultenaea arida*
- Geraniaceae
  - *Erodium cygnorum*
- Goodeniaceae
  - *Dampiera tenuicaulis*
  - *Goodenia dyeri*
  - *Scaevola bursariifolia*
  - *Scaevola spinescens*
- Haloragaceae
  - *Gonocarpus nodulosus*
- Lamiaceae
  - *Hemigenia teretiuscula*
  - *Prostanthera grylloana*
  - *Teucrium sessiliflorum*
  - *Westringia cephalantha*
  - *Westringia rigida*
- Lauraceae
  - *Cassytha glabella*
  - *Cassytha melantha*
  - *Cassytha racemosa*
- Loganiaceae
  - *Mitrasacme paradoxa*
- Loranthaceae
  - *Amyema miquelii*
- Mimosaceae
  - *Acacia acuminata*
  - *Acacia andrewsii*
  - *Acacia blaxellii* ms
  - *Acacia camptoclada*
  - *Acacia deficiens* ms
  - *Acacia duriuscula*
  - *Acacia erinacea*
  - *Acacia hadrophylla* ms
  - *Acacia hystrix*
  - *Acacia lasiocalyx*
  - *Acacia merrallii*
  - *Acacia myrtifolia*
  - *Acacia pachypoda*
  - *Acacia poliochroa*
  - *Acacia truculenta* ms
  - *Acacia* sp (NG & ML 1959)
  - *Acacia uncinella*
- Myoporaceae
  - *Diocirea microphylla* ms
  - *Eremophila alternifolia*
  - *Eremophila calorhabdos*
  - *Eremophila clavata* ms
  - *Eremophila decipiens*
  - *Eremophila densifolia* subsp *pubiflora*
  - *Eremophila deserti*
  - *Eremophila dichroantha*
  - *Eremophila interstans*
  - *Eremophila psilocalyx*
  - *Eremophila rugosa* ms
  - *Eremophila scoparia*
- Myrtaceae
  - *Astartea ambigua*
  - *Baeckea crispiflora*
  - *Calothamnus quadrifidus*
  - *Calytrix leschenaultii*
  - *Chamelaucium* sp (NG & ML 1963)
  - *Chamelaucium ciliatum*
  - *Chamelaucium megalopetalum*
  - *Eucalyptus annulata*
  - *Eucalyptus calycogona*
  - *Eucalyptus cerasiformis*
  - *Eucalyptus cylindriflora*
  - *Eucalyptus cylindrocarpa*
  - *Eucalyptus densa* subsp *densa*
  - *Eucalyptus dundasii*
  - *Eucalyptus eremophila*
  - *Eucalyptus flocktoniae*
  - *Eucalyptus georgei* subsp *georgei*
  - *Eucalyptus hypochlamydea* subsp *ecdysiastes* ms
  - *Eucalyptus incerata* ms
  - *Eucalyptus leptopoda*
  - *Eucalyptus livida*
  - *Eucalyptus longicornis*
  - *Eucalyptus longicornis x oleosa*
  - *Eucalyptus loxophleba*

Eucalyptus melanoxylon
Eucalyptus oleosa
Eucalyptus pileata
Eucalyptus platycorys
Eucalyptus rhomboidea ms
Eucalyptus salicola
Eucalyptus salmonophloia
Eucalyptus salubris
Eucalyptus sheathiana
Eucalyptus tenuis
Eucalyptus transcontinentalis
Eucalyptus yilgarnensis
Eucalyptus yilgarnensis x gracilis
Leptospermum fastigiatum
Melaleuca acuminata
Melaleuca cardiophylla
Melaleuca cliffortioides
Melaleuca cordata
Melaleuca coroniocarpa
Melaleuca eleuterostachya
Melaleuca fulgens
Melaleuca hamulosa
Melaleuca lanceolata
Melaleuca lateriflora
Melaleuca pauperiflora
Melaleuca pentagona
Melaleuca quadrifaria
Melaleuca sheathiana
Melaleuca phoidophylla ms
Melaleuca podicarpa ms
Melaleuca sp (NG & ML 2320)
Melaleuca sparsiflora
Melaleuca teuthidoides
Melaleuca torquata
Melaleuca uncinata
Micromyrtus obovata
Rinzia sessilis
Thryptomene australis
Thryptomene kochii

Orchidaceae
Caladenia microchila
Caladenia saccharata
Caladenia sigmoidea
Cyanicula caerulea
Genoplesium nigricans
Pterostylis mutica
Pterostylis sanguinea
Pterostylis sargentii
Thelymitra antennifera
Thelymitra aff *pauciflora*

Phormiaceae
Dianella revoluta

Pittosporaceae
Billardiera sp nov (NG & ML 1776)

Plantaginaceae
Plantago debilis
Plantago aff *hispidula* (NG & ML 1732)

Poaceae
* *Aira cupaniana*
Aristida contorta
Austrostipa elegantissima
Austrostipa platychaeta
Austrostipa scabra subsp *scabra*
Austrostipa trichophylla
Bromus arenarius
Danthonia caespitosa
Danthonia setacea var *setacea*
Neurachne alopecuroidea
* *Pentaschistis airoides*
Triodia scariosa
* *Vulpia bromoides*
* *Vulpia myuros*

Polygalaceae
Comesperma volubile

Portulacaceae
Calandrinia eremaea

Proteaceae
Grevillea acuaria
Grevillea huegelii
Grevillea oncogyne
Grevillea paradoxa
Grevillea pectinata
Grevillea teretifolia
Hakea commutata
Hakea cucullata
Hakea multilineata
Hakea scoparia
Persoonia helix

Rhamnaceae
Cryptandra minutifolia subsp *brevistyla*
Cryptandra polyclada
Pomaderris forrestiana
Stenanthemum intricatum
Stenanthemum pomaderroides
Trymalium myrtillus

Rubiaceae
Opercularia hispidula

Rutaceae
Boronia aff *fabianoides* (NG & ML 2313)
Boronia inornata subsp *inornata*
Boronia ternata var *ternata*
Eriostemon fitzgeraldii
Eriostemon pachyphyllus
Microcybe multiflora var *multiflora*
Phebalium filifolium
Phebalium megaphyllum ms
Phebalium tuberculosum

Santalaceae
Exocarpos aphyllus
Exocarpos sparteus
Santalum acuminatum

Sapindaceae
Dodonaea bursariifolia
Dodonaea caespitosa
Dodonaea lobulata
Dodonaea microzyga var *acrolobata*
Dodonaea stenozyga
Dodonaea viscosa subsp *angustissima*

Solanaceae
Anthocercis genistoides
Lycium australe
* *Solanum hystrix*

Sterculiaceae
Rulingia luteiflora

Stylidiaceae
Levenhookia pusilla

Urticaceae
Parietaria debilis

Zygophyllaceae
Zygophyllum apiculatum
Zygophyllum glaucum

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Flora and vegetation of the Eastern Goldfields Ranges: Part 3. Parker Range

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Abstract

A study of the flora and plant communities of the Parker Range greenstone belt recorded 254 taxa in the spring of 1994. Only 10 weed species were recorded but this number is likely to increase if further work is carried out in a better season. The flora list included new populations of eight rare or poorly known taxa. Of the five species apparently endemic to the Parker Range greenstone belt, two were collected for the first time.

Six community types were defined from 61 sites spread across the range. The distribution of these community types appears to be primarily controlled by edaphic factors including water holding capacity. Three of the floristic communities have some representation in conservation reserves but four of the endemic taxa and three of the community types are presently unreserved. The flora and community types of the Parker Range are significantly different from the Bremer Range (100 km to south east) although the local underlying ecological gradients appear to be similar. It is suggested that the differences between the range systems is related to regional climatic gradients. There has been significant impact on the vegetation of this range by mining and mineral exploration.

Introduction

The Parker Range greenstone belt lies some 15 km south east of Marvel Loch and is composed primarily of Archaean (2500 - 3700 My old) mafic and ultramafic rocks (generally termed greenstone) which has undergone some degree of metamorphosis. This belt includes the Parker Range proper stretching south some 30 km to Cheritons Find and includes the areas of the Toomey Hills to the east and Harris Find to the north east. This highly-prospected area has several active mines and a high level of exploration activity. While there has been a long history of detailed geological exploration in the area our knowledge of the flora and vegetation of the area is still poor. This series of papers is aimed at providing detailed floristic information on individual ranges (Gibson *et al.* 1997; Gibson & Lyons 1998). This paper reports recent survey work in the Parker Range greenstone belt.

Study Locality

The geology of the study area has been mapped and described by Gee (1982) and Bagas (1991). The Parker Range proper consists of a broad band of mafic rock with narrow band of banded ironstone on the eastern side, to the west is area of schist and phylite with some significant areas of laterization. A narrow band of massive gossan (concentrated iron minerals) runs north - south through Mt Caudan at the interface between the laterites and the schists (Bagas 1991). The Toomey Hills and Harris Find have similar geologies without occurrence of banded ironstone or gossan. Further away from the uplands outwash plains or sand plains occur. Overall the topography is subdued reflecting the great age of this landscape.

This region has cool winters and hot dry summers. The nearest climatic station is Southern Cross, some 50 km to the north west, which has a mean annual rainfall of 274 mm with temperature extremes from 47.2 °C to -5.0 °C (Newbey 1995).

Beard (1979) first described the major structural formations in the area. He grouped his structural units into vegetation systems and defined the vegetation of the Parker Range, Toomey Hill and Harris Find as forming the Parker Range System. From this system he described the woodlands of the bottom lands being commonly dominated by *Eucalyptus longicornis, E. salmonophloia,* and *E. salubris* with three types of understorey: *Atriplex, Melaleuca* or a mixed understorey of *Eremophila, Acacia,* and *Olearia muelleri.* On rising ground there are mallee or thicket communities primarily of *Acacia* spp and *Allocasuarina* spp, with ridge tops being dominated by thickets of *Eucalyptus redunca (= E. capillosa* subsp *polyclada), Allocasuarina campestris, Calothamnus chrysantherus* and a number of other species.

In the Boorabbin-Southern Cross report of the eastern goldfields regional survey, Newbey *et al.* (1995) described the undulating greenstone plain of the Parker Range. The colluvial flats of this unit are dominated by *Eucalyptus salubris* low woodland, with more basic soils dominated by *E. longicornis* low woodland. The understorey shrubs in these woodlands were normally *Melaleuca pauperiflora,*

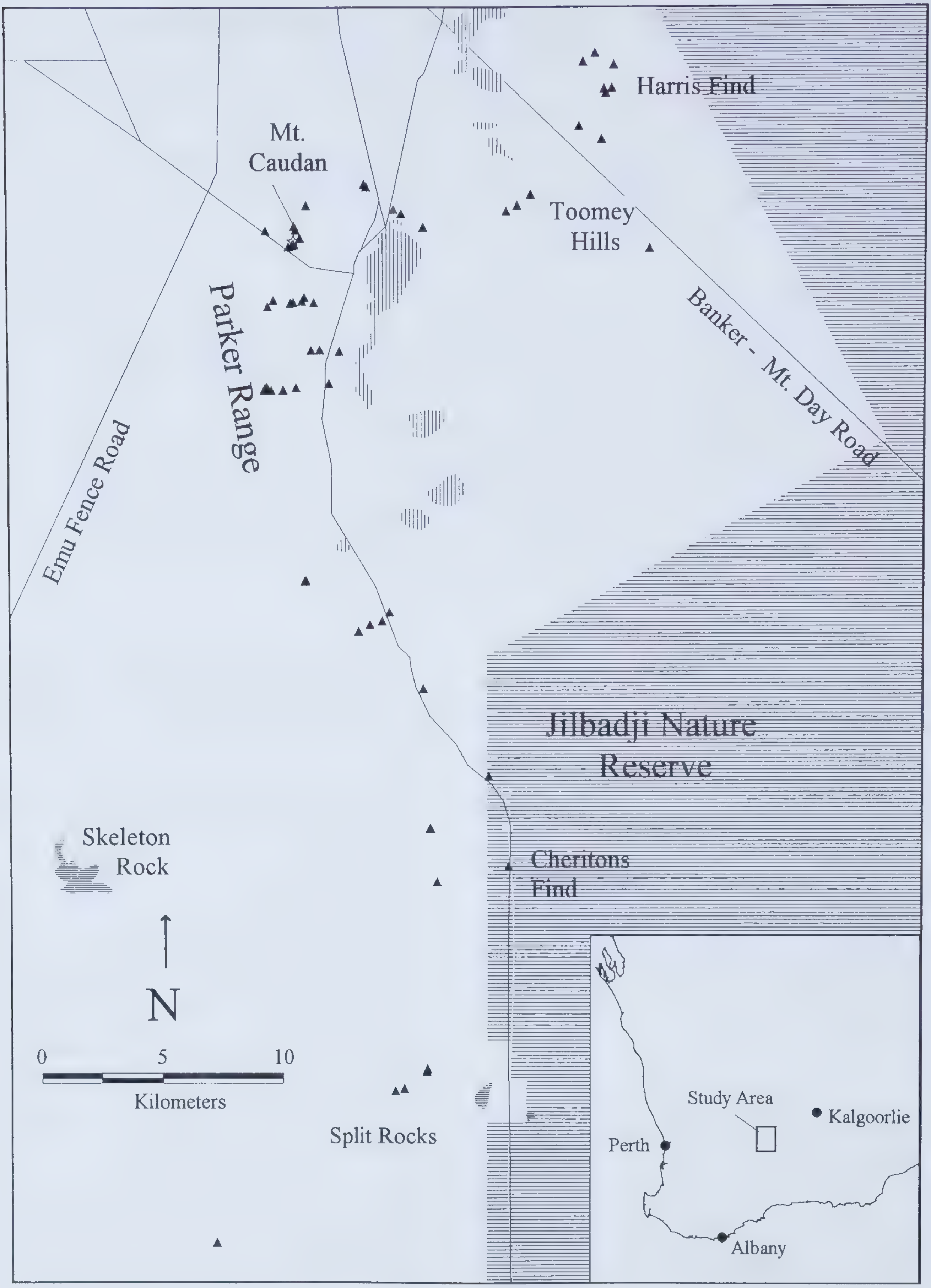

Figure 1. Location of study area. Individual sampling sites shown by solid triangles.

Exocarpos aphyllus, *Acacia merrallii* and *Templetonia sulcata*. On the low rises and ridges *E. longicornis* low woodland dominated on the shallow calcareous earths, with *E. corrugata* low woodland on stony rises and *E. conglobata* low woodland on the upper slopes. Growing with the *E. longicornis* were *Melaleuca pauperiflora*, and *Atriplex vesicaria*. They note that the gossanous cap (massive ironstone) of Mt Caudan and nearby ridges in the Parker Range supported a distinctive *Hakea pendens* tall shrubland. Both Beard's survey and the later biological survey of the eastern goldfields were undertaken to provide regional overviews. Consequently the individual greenstone ranges were not sampled extensively.

Methods

Sixty one 20 m x 20 m quadrats were established in the Parker Range area (Fig 1). The sites attempted to cover the major geographical, geomorphological and floristic variation. Care was taken to locate sites in the least disturbed vegetation available in the area being sampled. All sites were located in the undulating greenstone plain and banded ironstone hills units of Newbey (1995).

Within each site all vascular plants were recorded. The sites were only visited once during the spring of 1994. This was a poor year for annuals and it could be expected that the species richness of most sites would increase significantly if revisited during a good season. Data on topographical position, slope, aspect, vegetation structure and condition were collected from each site. Topographical position was scored on a subjective five point scale from ridge tops (1) to broad flats (4) to dunes beside salt lakes (5). Slope was scored on a one to three scale from flat (1) to steep (3). Aspect was recorded as one of 16 cardinal directions. Vegetation structure was recorded using Muir's (1977) classification.

All sites were permanently marked with four steel fence droppers and their positions determined using a GPS unit. Twenty four soil samples from the upper 10 cm were collected from each site. These were bulked and analysed for electrical conductivity, pH, total N, total P, percentage sand, silt and clay, exchangeable Ca, exchangeable Mg, and exchangeable K (Gibson *et al.* 1997).

Sites were classified according to similarities in species composition of perennial taxa. The 1994 season was quite poor and annuals and geophytes had a very patchy distribution. The classification undertaken used the Czekanowski coefficient and "unweighted pair-group mean average" fusion method (UPGMA; Sneath & Sokal 1973). Species were classified into groups according to their occurrence at the same sites by using the TWOSTEP similarity algorithm (Austin & Belbin 1982) followed by UPGMA fusion. Alternate classifications were tried using the ALOC algorithm (Belbin 1987). The resulting classifications were largely similar and only the former will be discussed in detail.

Semi-strong hybrid (SSH) ordination of the site data was undertaken to show spatial relationships between groups and to elucidate possible environmental correlates with the classification (Belbin 1991). Statistical relationships between site groups for such factors as species richness, soil parameters, slope, aspect, *etc*, were tested using Kruskal-Wallis non parametric analysis of variance and Mann Whitney U-tests (Siegel 1956).

Nomenclature follows Green (1985) and current usage at the Western Australian Herbarium. Selected voucher specimens will be lodged in the WA Herbarium.

Results

Flora

A total of 253 taxa (species, subspecies and varieties) and 1 hybrid were recorded from the 61 plots or the adjacent area. The best represented families were Myrtaceae (57 taxa), Asteraceae (23 taxa), Mimosaceae (20 taxa), Proteaceae (17 taxa), Poaceae (15 taxa) and the Chenopodiaceae (14 taxa). The composition of the flora on the range was very similar to, and typical of, the flora of the South Western Interzone (Newbey *et al.* 1995).

The most common genera were *Eucalyptus* (29 taxa), *Acacia* (20 taxa), *Melaleuca* (13 taxa), and *Grevillea* (8 taxa). Annual weed species were rarely encountered (only 10 recorded) resulting from the below average rainfall of the 1994 season. During the survey new populations of eight rare or poorly known taxa being considered for gazettal as Declared Rare Flora were located (K Atkins, CALM, *pers comm*; Table 1).

Table 1

The number of new populations of species being considered for gazettal as Declared Rare Flora found during the survey (K Atkins, CALM, pers comm).

Taxon	Number of new populations
Acacia asepala ms	4
Acacia concolorans ms	8
Acrotriche patula	3
Drummondita wilsonii	1
Gnephosis intonsa	2
Grevillea phillipsiana	4
Hakea pendens	15
Hemigenia obovata	1

The survey significantly extended the known range of *Hakea pendens* which was previously known only from the top of Mt Caudan and the nearby ridges with massive gossanous caps (Newbey *et al.* 1995). It was found to be much more widespread than previously thought, being common on lateritic ridge tops of this greenstone belt extending south to Cheriton's Find and north east to Harris Find.

An undescribed subspecies of *Chamelaucium halophilum* ms has been collected from Mt Caudan on three occasions, first by B Smith in 1989, and subsequently by G Keighery and during this survey. This deep pink flowered shrub is considered quite distinct from typical *Chamelaucium halophilum* ms and awaits formal description as a subspecies (GJ Keighery, CALM, personal communication).

Two other undescribed taxa were collected for the first time. *Euryomyrtus ciliata* ms was collected from three populations in the Parker Range and will be described in the forthcoming revision (M Trudgen, DEP, personal communication). Also in the Parker Range the large pink flowered *Isopogon robusta* ms related to *Isopogon scabriusculus* was collected from a single population on sheet laterite only some 15 m off a major mining exploration track.

Chamelaucium halophilum subsp nov, *Drummondita wilsonii*, *Euryomyrtus ciliata* ms, *Hakea pendens*, and *Isopogon robusta* ms appear to be endemic to the Harris Find-Parker Range-Cheritons Find greenstone belt. The present survey recorded 49 additional taxa for the Parker Range area (*cf* Newbey *et al.* 1995). Some of these additions are a result of improvement in taxonomic knowledge.

Vegetation

Some species had to be amalgamated into complexes for the floristic analysis due to difficulty of differentiating between closely related taxa without good flowering material (e.g. *Hibbertia rostellata* complex and the *Melaleuca pauperiflora* complex). One hundred and seventy one perennial taxa were recorded from the 61 quadrats located in the Parker Range greenstone belt. Fifty eight taxa occurred at only one site. These singletons have little effect on the community classification and were excluded, so the final data set consisted of 113 taxa by 61 sites. Species richness ranged from 6 to 29 taxa per site, with individual taxa occurring in between 2 and 29 sites. Site groups are discussed at the six group level which best reflected the scale of patterning seen in the field.

The primary division seen in the dendrogram (Fig 2) separates the sites occurring on the deeper more fertile soils (types 1 to 3) from sites occurring on greenstone and lateritic ridges (types 4 to 6). This can also be seen in the sorted two way table of the site and species classifications (Table 2). The first three community types are eucalypt woodlands while the last three include both woodland and thicket communities.

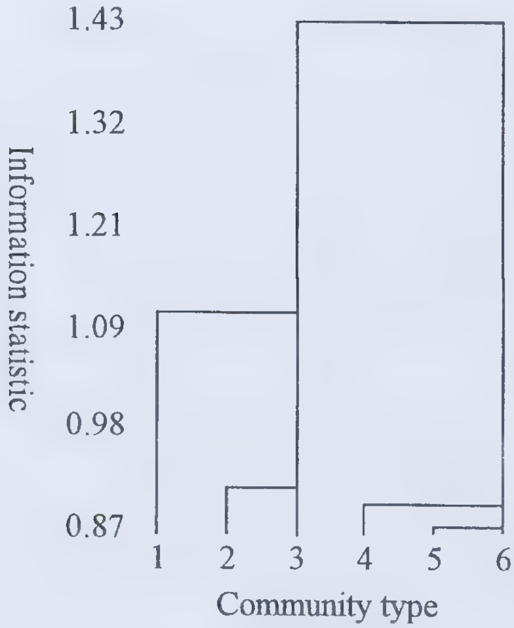

Figure 2. Dendrogram of the floristic sites from the Parker Range area showing the six group level classification.

- **Community type 1** occupies the sandy soils at the base of ridges and low rises. It had the highest mean species richness of 17.4 taxa /plot. It is generally dominated by *Eucalyptus sheathiana* with *E. transcontinentalis* and /or *E. eremophila* as co-dominants. The most typical understorey species were *Daviesia argillacea* and *Grevillea huegelii.* Species groups I and J were the most faithful to this community type. It also shared species of group A with the three upland community types (types 4 to 6).
- **Community type 2** was generally dominated *Eucalyptus longicornis.* Other eucalypts that occurred as co-dominants included *E. corrugata* and *E. salubris.* At one site this community was dominated by *E. myriadena.* This community occupied the broad flats with species from group G being the most typical. Mean species richness was quite low at 10.0 taxa /plot.
- **Community type 3** also occurred on the broad flats within the greenstone belt. It was usually dominated by *Eucalyptus salmonophloia* and *E. salubris.* Typical understorey species of this community include *Eremophila oppositifolia, Acacia concolorans* ms, *Dodonaea stenozyga* and *Scaevola spinescens.* It had a higher mean species richness (12.9) than type 2 (10.0). Species patterning in groups A and G suggests that further subdivision into a northern and a southern subgroup is possible (Table 2).

The three remaining community types are those typical of the lateritic and greenstone ridges. Differences in species frequency in species groups A, B, C, D and F differentiate between them. Community type 4 tends to occur on the deeper sandy soils, type 5 on somewhat more skeletal soils and type 6 on massive greenstone. Mean species richness was similar in community types 4 and 5 (14.8 & 15.5) but quite low in type 6 (9.5 taxa /plot).

- **Community type 4** was generally dominated by *Allocasuarina acutivalvis* and *Allocasuarina corniculata.* At some sites *Eucalyptus capillosa* subsp *polyclada* also occurred, but this species was more typical of community type 5. Other species typical of this community type included *Baeckea elderiana* and *Thryptomene kochii,* further illustrating the sandy nature of these sites.
- **Community type 5** almost totally lacked *Allocasuarina corniculata* (*cf* type 4), being replaced by *A. campestris,* while *Allocasuarina acutivalvis* was still a common element. *Eucalyptus capillosa* subsp *polyclada* and /or *Eucalyptus loxophleba* tended to dominate these sites while *Hakea pendens, Phebalium tuberculosum,* and *Westringia cephalantha* were common understorey elements. This community type was associated with laterites, breakaways and the massive gossanous caps of the Mt Caudan area.
- **Community type 6** was restricted to a small area of a massive decomposing laterite and granite in the Parker Range. The area was dominated by low trees of *Callitris glaucophylla* and the previously unknown *Isopogon robusta* ms.

Environmental correlates

Correlation with soil and geomorphological parameters. Soil parameters in particular showed high levels of intercorrelation (Table 3). Some care needs to be taken in interpreting comparisons with community type 6 since only two quadrats of this community were sampled. Altitude

Table 2

Sorted two way table of the Parker Range greenstone sites showing species occurrence by community type. Site appear as columns, species as rows

	COMMUNITY TYPE					
	1	2	3	4	5	6
TAXA						
Species Group A						
Acacia acuminata	*		*	*** **	* * ****	
Allocasuarina acutivalvis	* *		*	**** ****	* ** ** *	
Eucalyptus capillosa subsp *polyclada*	** *		*	** *	** ***	*
Hakea pendens	* *			*	** ****	
Phebalium tuberculosum	*		* **	* **	*** *** *	*
Comesperma volubile	*			**	***	**
Micromyrtus racemosa			*	* *	** * *	*
Allocasuarina campestris				*	***** **	
Trymalium myrtillus			* *	*	** *	*
Hibbertia exasperata	*			*	* *	
Acacia hemiteles	* *		* **	*	*	
Lepidosperma sp (GJK 7000)	*			*	* * *	
Melaleuca eleuterostachya	* *			*	**	
Eucalyptus loxophleba	*			*	* ***	
Melaleuca uncinata	** **		*	* **	** **	**
Westringia cephalantha	*** ***		*	*	* ** ***	
Phebalium filifolium	**		*	*	* ***	
Species Group B						
Acrotriche patula	*				*	*
Borya constricta			*		*	*
Cheilanthes austrotenuifolia					* *****	
Eremophila granitica					* *	
Prostanthera incurvata			*	*	*	
Callitris glaucophylla				*		**
Lepidosperma sp				*		*
Species Group C						
Acacia fragilis					**	
Hakea subsulcata				*	** *	
Cassytha filiformis				*	*	
Astroloma serratifolium				*	*	
Acacia neurophylla				*** *	* *	
Calothamnus gilesii				*** **	* *** * *	
Grevillea obliquistigma				* ****	*** ** ***	
Hibbertia rostellata				*********	******* **	*
Allocasuarina corniculata				***** ***	*	
Baeckea elderiana				* *******	*	
Grevillea paradoxa	*			*******	* ***	
Melaleuca cordata	*			* *** * *	* **	
Cassytha glabella	*			****		
Thryptomene kochii	**			** ***		
Eucalyptus burracoppinensis				* *	*	
Eucalyptus leptopoda				**		
Melaleuca cardiophylla				** *		
Micromyrtus maidenii				*** *		
Species Group D						
Eucalyptus livida				* *	*	
Hakea francisiana	*			* *		
Euryomyrtus ciliata ms			*	*		
Species Group E						
Grevillea oncogyne	*			*		
Hibbertia pungens	*				*	
Species Group F						
Acacia colletioides			*		*	
Dodonaea bursariifolia					**	
Dodonaea microzyga var *acrolobata*					** * *	
Eucalyptus capillosa subsp *capillosa*					* *	
Eremophila decipiens		* *	*		*	
Olearia pimeleoides	*		*		* *	
Eucalyptus corrugata			* *		**	
Eucalyptus oleosa			*		* *	

Table 2 (continued)

	COMMUNITY TYPE					
	1	2	3	4	5	6
Species Group G						
Acacia asepala ms		** * *				
Eucalyptus conglobata		***				
Eucalyptus calycogona	*	*	**			
Acacia pachypoda		**				
Atriplex vesicaria		****	**			
Eucalyptus melanoxylon		*	*			
Eremophila scoparia		** *****	** *****			
Sclerolaena diacantha		***	************			
Templetonia sulcata		* ******	******* *			
Eucalyptus longicornis		*********	****		*	
Zygophyllum glaucum		* **	*			
Eucalyptus yilgarnensis			* *** *			
Grevillea phillipsiana		*	***			
Lycium australe		**	*			
Maireana radiata			* *			
Zygophyllum apiculatum		*	*			
Maireana trichoptera			* **			
Rhagodia drummondii		*	* *** *			
Ptilotus holosericeus			* * * *			
Acacia poliochroa			**			
Cassia nemophila		*			*	
Species Group H						
Acacia concolorans ms	* *		* *** * *			
Eremophila oppositifolia			* ***** * *** *		*	*
Eucalyptus salmonophloia	*		************		*	
Acacia erinacea	* *	*	*** * ** **** *	*	** *	
Olearia muelleri	* ***	** * *	* ** * ** * *****		* *	*
Eucalyptus salubris	**	* * *	*** * ***** *** **	*		
Exocarpos aphyllus	* *	*	** ** * ** ***			
Scaevola spinescens	* *		* ** ** *** ***		**	
Austrostipa elegantissima	**	*** *** *	***** **********		*** * *	
Acacia merrallii	*	***** * **	* ** *** * *	*	*	
Melaleuca pauperiflora	* * **	*** ** ***	** ******** *** *		*	
Eremophila ionantha	*	* **	* * *** *			
Amyema miquelii	*	* *	* * * *		*	
Dodonaea stenozyga		*	*** ** * *		*	
Alyxia buxifolia	**		** * * * * ****		*** ** ***	**
Santalum acuminatum	*****	** * *	* ** *	** **	** ** *	
Beyeria brevifolia		*	***	**	* *	
Species Group I						
Acacia camptoclada	**		*		*	
Melaleuca lateriflora	* *		***			
Ptilotus gaudichaudii	*		**		*	
Daviesia argillacea	*******	*	* *	*		
Eucalyptus sheathiana	***** *		*		*	
Melaleuca acuminata	*** *		** *	*		
Eucalyptus eremophila	* ***					
Eremophila drummondii	*		* *			
Grevillea huegelii	* ** **		*			
Grevillea acuaria	* *		* *	*		
Eucalyptus transcontinentalis	***	* *	* * *			
Phebalium megaphyllum ms	***			*		*
Species Group J						
Cassytha melantha	***					
Melaleuca ureolaris ms	**					
Dianella revoluta	*				*	
Species Group K						
Eremophila saligna	*				*	
Lomandra effusa	*	*			*	
Melaleuca sp (NG & ML 2335)	*	*				
Ptilotus drummondii	*		*			
Microcybe multiflora var *multiflora*	*		* * **			

Table 3

Matrix of Spearman rank correlation coefficients between environmental parameters. Only correlations significant at $P < 0.01$ shown ($r \geqslant 0.3325$). See methods for soil parameter codes.

	Altitude	Aspect	Ca	Clay	Conduct	K	Mg	Na	Total N	pH	Total P	Sand	Silt	Slope	Topog
Altitude	1.000														
Aspect		1.000													
Ca	-0.408		1.000												
Clay			0.413	1.000											
Conduct			0.714	0.551	1.000										
K	-0.514		0.822		0.661	1.000									
Mg	-0.356		0.838	0.527	0.781	0.862	1.000								
Na			0.632	0.601	0.929	0.676	0.843	1.000							
Total N			0.766	0.338	0.732	0.551	0.603	0.594	1.000						
PH	-0.495		0.840		0.593	0.904	0.816	0.576	0.514	1.000					
Total P	-0.354		0.475			0.422			0.540		1.000				
Sand			-0.674	-0.853	-0.772	-0.602	-0.748	-0.760	-0.618	-0.528		1.000			
Silt	-0.383		0.791	0.429	0.729	0.777	0.779	0.677	0.738	0.730	0.342	-0.800	1.000		
Slope		0.662												1.000	
Topog	-0.365		0.410			0.563	0.485	0.396		0.524			0.418		1.000

Table 4.

Parker Range community type means for altitude, topographic position (1-ridge top to 4-valley flat), slope class (1-flat to 3-steep), aspect (16 cardinal directions) and species richness. Non significant differences between means indicated by same superscript ($P>0.05$, Mann-Whitney U-test).

Community Type	Altitude (m)	Topography	Slope	Aspect	Species richness
1	417.1^{ab}	3.0^{ab}	1.6^{a}	1.6^{a}	17.4^{abc}
2	391.0	3.7^{bc}	1.5^{a}	2.2^{a}	10.0^{b}
3	401.9^{ab}	3.7^{bc}	1.8^{a}	3.5^{a}	12.9^{ce}
4	415.6^{b}	2.9^{a}	1.8^{a}	3.3^{a}	14.8^{cd}
5	403.3^{ab}	2.8^{a}	2.0^{b}	4.0^{a}	15.5^{d}
6	420.0^{b}	2.5^{a}	2.0^{b}	4.8^{a}	9.5^{abe}

Table 5.

Parker Range community type means for soil parameters. Non significant differences between means indicated by same superscript ($P>0.05$, Mann-Whitney U-test).

Community Type	Electrical Conductivity (mS m^{-1})	pH	N total (%)	P total (%)	% Sand	% Silt	% Clay	Exchangeable Ca (me %)	Exchangeable Mg (me %)	Exchangeable Na (me %)	Exchangeable K (me %)
1	5.9^{a}	6.40^{a}	0.038^{a}	64.9^{ac}	82.6^{a}	5.1^{a}	12.3^{a}	2.9^{a}	1.80^{a}	0.27^{a}	0.31^{a}
2	31.6^{b}	8.27	0.127^{b}	105.3^{bd}	65.0^{b}	19.3^{b}	15.8^{a}	14.8^{b}	5.47^{b}	0.90^{b}	1.63
3	21.6^{c}	7.72	0.089^{c}	86.8^{ab}	65.3^{b}	13.1^{c}	21.6	11.9^{bc}	6.02^{b}	1.05^{b}	0.88
4	3.6^{a}	5.46^{b}	0.052^{d}	51.3^{ce}	79.6^{a}	6.7^{ad}	13.8^{a}	1.9^{d}	0.64^{c}	0.10^{c}	0.19^{b}
5	6.1^{ad}	6.33^{a}	0.081^{cd}	142.3^{d}	79.1^{a}	7.5^{ad}	13.4^{a}	5.1^{e}	1.34^{a}	0.21^{acd}	0.27^{ac}
6	27.5^{bcd}	5.10^{ab}	0.075^{abcd}	60.0^{abe}	54.8^{b}	10.0^{bcd}	35.3	3.8^{acde}	1.98^{abc}	0.83^{bd}	0.15^{bc}

and topographic class were found to be significantly correlated with six of the soil parameters and with each other (Table 3). Percentage silt was more highly correlated with soil nutrient parameters than was percentage clay. There were significant differences between floristic group means for some of the geomorphical parameters (Table 4) and for most of the soil parameters measured (Table 5).

Topographic position clearly separated the upland community types (types 4 to 6) from the other vegetation types. Differences in mean altitude were not as clear, while community types 5 and 6 occurred on steeper slopes than community type 4 (Table 4). Within the lowland communities, community type 2 occurred at a significant lower altitude than types 1 and 3 (Table 4).

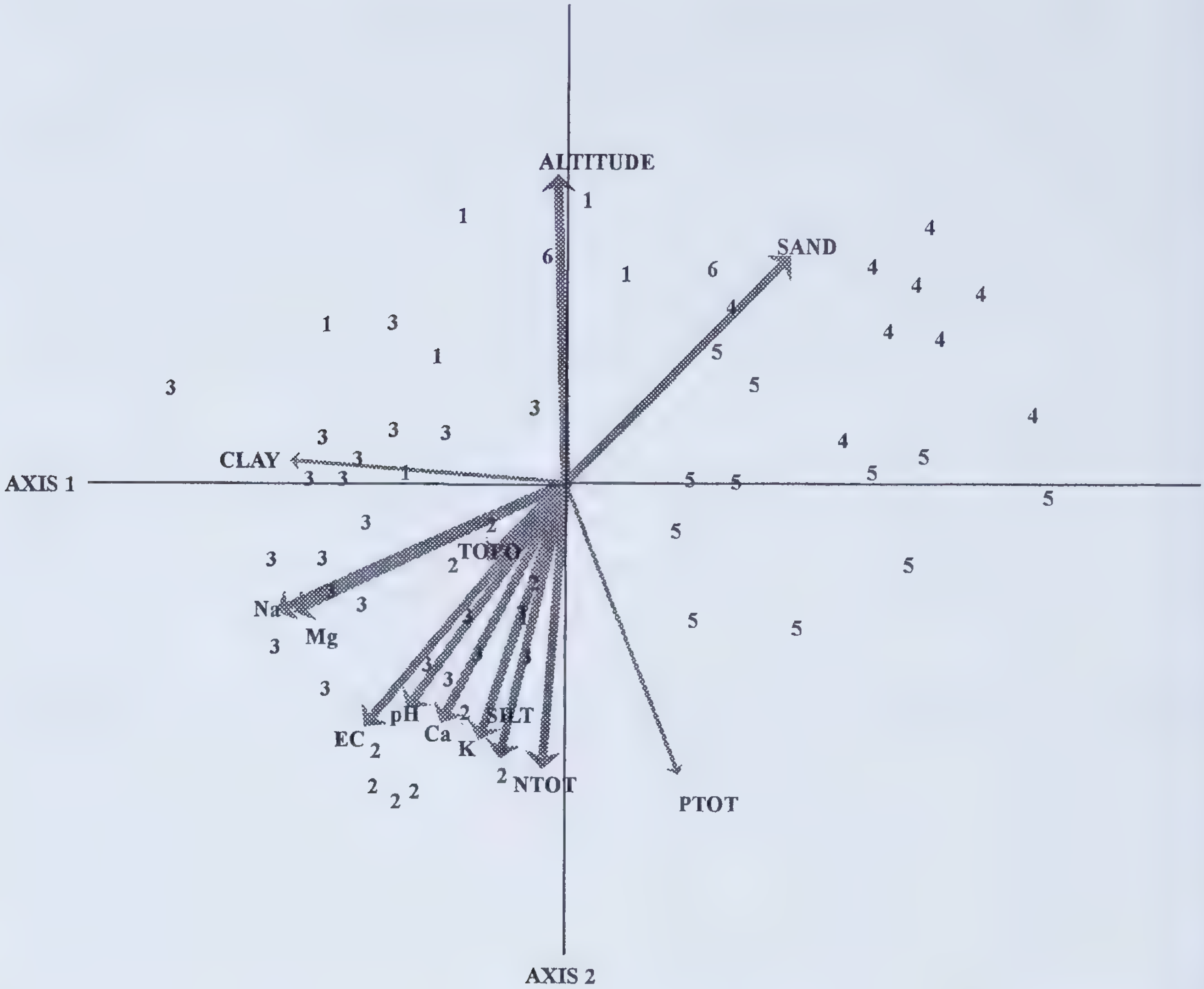

Figure 3. Ordination of Parker Range floristic sites with numbers corresponding to community types. Arrows show the direction of the best fit linear correlation for environmental parameters. Narrow arrows are significant at $P < 0.05$, and broad arrows at $P < 0.01$, $n = 61$.

Of the lowland community types the *Eucalyptus sheathiana-E. eremophila* community (type 1) occurred on soils with significantly higher percentage sand and lower pH than the other two types. These soils were also significantly lower in total N, and exchangeable Ca, Mg, Na, and K and had very low electrical conductivity compared to community types 2 and 3. Total P was also lower lower than community type 3 (Table 4).

The soils of the *Eucalyptus salmonophloia-E. salubris* flats (type 3) and the *E. longicornis* flats (type 2) had high electrical conductivity, and significantly higher pH than any other community type. Both community types had high levels of all soil nutrient parameters measured. The *E. longicornis* flats (type 2) had significantly higher pH (8.27) than the *Eucalyptus salmonophloia - E. salubris* flats (type 3) (7.72) while this latter community type occurred on soils with significantly greater clay content (22% *cf* 16%) (Table 4).

Comparisons of community type 6 with the other two upland community types is difficult due to the small number (two) of quadrats sampled. Community type 6 was found only in a very localised area on the Parker Range. The soils at these site were skeletal over massive laterite and decomposing granite and showed very high clay content (Table 4).

The other two upland community types show radically different soil chemistry. Soils of community type 5 showed significantly higher pH, total P, exchangeable Ca, Mg, and K than community type 4. Soil mechanical analysis, however, showed a similar breakdown of sand, silt and clay. Community type 4 tended to occur on deep yellow soils compared to the shallower brown soils of community type 5.

Ordination results. The Parker Range sites were ordinated to show spatial relationships between groups and to better elucidate possible environmental correlates with the classification. A three dimensional solution with a stress level of 0.21 was used. Superimposed on the ordination output (Fig 3) are best fit linear correlations of the environmental parameters measured using principal axis correlation (Belbin 1993). All parameters were range standardised prior to fitting.

The ordination shows a clear separation between the ridge top communities (types 4, 5 & 6) and the lower slope communities (types 1, 2 & 3). The least fertile, most sandy woodland community (type 1), is clearly most closely related to the upland thickets and woodlands (types 4, 5 & 6) (Figure 3). Soil nutrient status was again the most obvious environmental gradient. The plot also suggests altitude and perhaps percentage sand as being another significant gradient divergent from the soil nutrient axis. This could be interpreted as a soil moisture or moisture availability gradient. The stronger correlation of percentage silt (*cf* percentage clay) with soil nutrient parameters can be clearly seen (Fig 3).

Discussion

Our present poor knowledge of the flora and vegetation patterning of the Parker Range greenstone belt is highlighted by the discovery of two previously unknown taxa (*Euryomyrtus ciliata* ms & *Isopogon robusta* ms), the large range extension documented for *Hakea pendens*, and the location of new populations of eight rare or poorly known taxa (K Atkins, CALM, *pers comm*; Table 1) during a 10 day period.

Five taxa appear to be endemic to the Parker Range. Similar levels of endemism have been reported for the Helena and Aurora Range and the Bremer Range (Gibson *et al.* 1997). This endemism is not related to ultramafic substrates which are often associated with high levels of endemism elsewhere (Brooks 1987). The ranges may have acted as refugia during the waves of aridity of the Tertiary which is now reflected by patterns of local endemism (Hopper 1979).

There is a marked change over in the flora between the Bremer Range and the Parker Range even though these ranges are only 100 km apart. Of the combined flora list of 396 taxa, 141 were recorded only on the Bremer Range and 127 were recorded only on the Parker Range. Within the major genera a similar pattern is seen. A total of 40 eucalypt species were recorded from the two range systems, 19 were shared, 11 were recorded only from the Bremer Range and 10 were recorded only from the Parker Range.

Six community types were described for the Parker Range greenstone belt. The distribution of these communities appears to be primarily controlled by edaphic factors and soil water capacity. Soil development is strongly correlated to altitude and topographic position. These relationships were not as pronounced in the Bremer Range (Gibson & Lyons 1998) where topography is much more subdued. The ridge tops of laterites, schists and greenstones generally had a much lower soil nutrient status than the alluvial and colluvial deposits of the valley bottoms.

A similar cantena of vegetation types has been reported from the Bremer Range (Gibson & Lyons 1998) however the species composition of the two cantenas is significantly different, as could be expected from the change over in the flora described above. Soil chemistry between the two range systems is similar (as shown by a classification of site soil data) and cannot account for the major differences in flora and community types. It is likely that the flora is changing in relation to regional scale climatic gradients.

The previous work undertaken in the study area described broad regional vegetation patterns (Beard 1979; Newbey *et al.* 1995). Our results are consistent with those descriptions but suggest a much more complex mosaic of vegetation patterning and support Beard's concepts of the Parker Range Vegetation System (Beard 1979). One of the vegetation communities showed some north - south subdivision, another one was very localised while the remaining four were spread throughout the different greenstone belts.

The Cheritons Find area lies just within Jilbadgi Nature Reserve and three of the six Parker Range vegetation types were recorded from this area as was *Hakea pendens*. The other three community types and the four endemic taxa are unreserved. The area of the Parker Vegetation System in reserves (106 km^2 in reserves out of a total of 800 km^2) is much less than earlier suggested by Newbey *et al.*(1995) since much of area mapped as this vegetation system in Jilbadgi Nature Reserve is in fact Tertiary sandplain (Bagas 1991). None of the three communities occurring in Jilbadgi Nature Reserve could be considered well reserved.

Mining and exploration activity have significantly impacted on the vegetation of this area. The most obvious example of this is Mt Caudan where exploration gridding has been extensive and where clean up (including capping of drill holes) has been minimal. Two taxa endemic to this greenstone belt occur in this area and one is restricted to it.

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Appendix 1

Flora list for the Parker Range greenstone belt (* indicates introduced taxa).

- Adiantaceae
  - *Cheilanthes austrotenuifolia*
- Aizoaceae
  - * *Mesembryanthemum nodiflorum*
- Amaranthaceae
  - *Ptilotus drummondii*
  - *Ptilotus exaltatus*
  - *Ptilotus gaudichaudii*
  - *Ptilotus holosericeus*
- Anthericaceae
  - *Borya constricta*
  - *Thysanotus patersonii*
- Apiaceae
  - *Daucus glochidiatus*
  - *Trachymene cyanopetala*
  - *Trachymene ornata*
- Apocynaceae
  - *Alyxia buxifolia*
- Asteraceae
  - *Angianthus tomentosus*
  - * *Arctotheca calendula*
  - *Asteridea athrixioides*
  - *Brachyscome iberidifolia*
  - *Gnephosis intonsa*
  - *Hyalosperma glutinosum* subsp *glutinosum*
  - * *Hypochaeris glabra*
  - *Lawrencella rosea*
  - *Leucochrysum fitzgibbonii*
  - *Millotia tenuifolia*
  - *Olearia exiguifolia*
  - *Olearia muelleri*
  - *Olearia pimeleoides*
  - *Podolepis capillaris*
  - *Podolepis tepperi*
  - *Rhodanthe oppositifolia subsp oppositifolia*
  - *Rhodanthe rubella*
  - *Senecio glossanthus*
  - * *Sonchus oleraceus*
  - * *Ursinia anthemoides*
  - *Vittadinia triloba*
  - *Waitzia acuminata*
  - *Waitzia citrina*
- Boraginaceae
  - *Omphalolappula concava*
- Brassicaceae
  - *Stenopetalum lineare*
- Caesalpiniaceae
  - *Cassia nemophila*
- Campanulaceae
  - *Wahlenbergia preissii*
- Casuarinaceae
  - *Allocasuarina acutivalvis*
  - *Allocasuarina campestris*
  - *Allocasuarina corniculata*
  - *Allocasuarina helmsii*
- Chenopodiaceae
  - *Atriplex acutibractea* subsp *karoniensis*
  - *Atriplex vesicaria*
  - *Chenopodium curvispicatum*
  - *Eriochiton sclerolaenoides*
  - *Halosarcia halocnemoides*
  - *Maireana marginata*
  - *Maireana pentagona*
  - *Maireana radiata*
  - *Maireana trichoptera*
  - *Rhagodia drummondii*
  - *Sclerolaena convexula*
  - *Sclerolaena diacantha*
  - *Sclerolaena drummondii*
  - *Sclerostegia disarticulata*
- Convolvulaceae
  - *Wilsonia humilis*
- Crassulaceae
  - *Crassula colorata*
- Cupressaceae
  - *Callitris canescens*
  - *Callitris glaucophylla*
  - *Callitris preissii*
- Cyperaceae
  - *Lepidosperma* sp (GJK 7000)
  - *Lepidosperma* sp (KRN 7035)
  - *Lepidosperma* sp (NG & ML 2075)
  - *Schoenus nanus*
  - *Tetraria capillaris*
- Dasypogonaceae
  - *Chamaexeros macranthera*
  - *Lomandra effusa*
- Dilleniaceae
  - *Hibbertia exasperata*
  - *Hibbertia glomerosa*
  - *Hibbertia pungens*
  - *Hibbertia rostellata*
- Droseraceae
  - *Drosera macrantha* subsp *eremaea*
- Epacridaceae
  - *Acrotriche patula*
  - *Astroloma serratifolium*
- Euphorbiaceae
  - *Beyeria brevifolia*
  - *Poranthera microphylla*
- Fabaceae
  - *Daviesia argillacea*
  - *Eutaxia* sp (NG & ML 1997)
  - *Gastrolobium parviflorum*
  - *Gompholobium* sp (NG & ML 2292)
  - *Templetonia sulcata*
- Frankeniaceae
  - *Frankenia* sp (NG & ML 2031)
- Geraniaceae
  - *Erodium cygnorum*
- Goodeniaceae
  - *Goodenia havilandii*
  - *Goodenia* sp (NG & ML 2250)
  - *Goodenia* sp (NG & ML 2370)
  - *Goodenia* sp (NG & ML 2371)
  - *Scaevola spinescens*
- Haloragaceae
  - *Glischrocaryon aureum*
- Juncaginaceae
  - *Triglochin centrocarpum*
- Lamiaceae
  - *Hemigenia obovata*
  - *Prostanthera incurvata*
  - *Westringia cephalantha*
- Lauraceae
  - *Cassytha filiformis*
  - *Cassytha glabella*
  - *Cassytha melantha*
- Lobeliaceae
  - *Lobelia gibbosa*
- Loganiaceae
  - *Mitrasacme paradoxa*
- Loranthaceae
  - *Amyema miquelii*

- Mimosaceae
  - *Acacia acuminata*
  - *Acacia asepala* ms
  - *Acacia assimilis*
  - *Acacia camptoclada*
  - *Acacia colletioides*
  - *Acacia concolorans* ms
  - *Acacia deficiens* ms
  - *Acacia enervia*
  - *Acacia erinacea*
  - *Acacia fragilis*
  - *Acacia hemiteles*
  - *Acacia longispinea*
  - *Acacia merrallii*
  - *Acacia myrtifolia*
  - *Acacia neurophylla*
  - *Acacia nigripilosa*
  - *Acacia nyssophylla*
  - *Acacia pachypoda*
  - *Acacia poliochroa*
  - *Acacia rendlei*
- Myoporaceae
  - *Eremophila decipiens*
  - *Eremophila drummondii*
  - *Eremophila granitica*
  - *Eremophila ionantha*
  - *Eremophila oppositifolia*
  - *Eremophila saligna*
  - *Eremophila scoparia*
  - *Myoporum tetrandrum*
- Myrtaceae
  - *Baeckea crispiflora*
  - *Baeckea elderiana*
  - *Baeckea grandibracteata*
  - *Beaufortia orbifolia*
  - *Calothamnus gilesii*
  - *Calytrix breviseta* subsp *stipulosa*
  - *Chamelaucium halophilum* subsp nov
  - *Eucalyptus annulata*
  - *Eucalyptus burracoppinensis*
  - *Eucalyptus calycogona*
  - *Eucalyptus capillosa* subsp *capillosa*
  - *Eucalyptus capillosa* subsp *polyclada*
  - *Eucalyptus conglobata*
  - *Eucalyptus corrugata*
  - *Eucalyptus cylindriflora*
  - *Eucalyptus cylindrocarpa*
  - *Eucalyptus eremophila*
  - *Eucalyptus flocktoniae*
  - *Eucalyptus gracilis*
  - *Eucalyptus hypochlamydea* subsp *ecdysiastes* ms
  - *Eucalyptus kondininensis*
  - *Eucalyptus leptopoda*
  - *Eucalyptus livida*
  - *Eucalyptus longicornis*
  - *Eucalyptus loxophleba*
  - *Eucalyptus melanoxylon*
  - *Eucalyptus myriadena*
  - *Eucalyptus oleosa*
  - *Eucalyptus platycorys*
  - *Eucalyptus rigidula*
  - *Eucalyptus salmonophloia*
  - *Eucalyptus salubris*
  - *Eucalyptus sheathiana*
  - *Eucalyptus spathulata* subsp *grandiflora*
  - *Eucalyptus transcontinentalis*
  - *Eucalyptus yilgarnensis*
  - *Euryomyrtus ciliata* ms
  - *Leptospermum roei*
  - *Melaleuca acuminata*
  - *Melaleuca cardiophylla*
  - *Melaleuca cordata*
  - *Melaleuca ctenoides*
  - *Melaleuca eleuterostachya*
  - *Melaleuca hamulosa*
  - *Melaleuca lateriflora*
  - *Melaleuca laxiflora*
  - *Melaleuca pauperiflora* subsp nov (NG 10)
  - *Melaleuca phoidophlla* ms
  - *Melaleuca* sp (NG & ML 2335)
  - *Melaleuca uncinata*
  - *Melaleuca ureolaris* ms
  - *Micromyrtus maidenii*
  - *Micromyrtus obovata*
  - *Micromyrtus racemosa*
  - *Thryptomene australis*
  - *Thryptomene kochii*
  - *Verticordia multiflora* subsp *solox*
- Orchidaceae
  - *Pterostylis* aff. *rufa*
  - *Pterostylis ciliata*
  - *Pterostylis mutica*
  - *Pterostylis roensis*
  - *Pterostylis sargentii*
  - *Thelymitra* aff. *pauciflora*
  - *Thelymitra sargentii*
- Phormiaceae
  - *Dianella revoluta*
- Plantaginaceae
  - *Plantago debilis*
- Poaceae
  - * *Aira cupaniana*
  - *Amphipogon strictus*
  - *Aristida contorta*
  - *Austrostipa elegantissima*
  - *Austrostipa hemipogon*
  - *Austrostipa* sp (NG & ML 2120)
  - *Austrostipa trichophylla*
  - *Bromus arenarius*
  - * *Bromus rubens*
  - *Danthonia acerosa*
  - *Danthonia caespitosa*
  - *Danthonia setacea*
  - *Triodia scariosa*
  - * *Vulpia bromoides*
  - * *Vulpia myuros*
- Polygalaceae
  - *Comesperma volubile*
- Portulacaceae
  - *Calandrinia eremaea*
  - *Calandrinia granulifera*
- Primulaceae
  - * *Anagallis arvensis*
- Proteaceae
  - *Adenanthos argyreus*
  - *Grevillea acuaria*
  - *Grevillea huegelii*
  - *Grevillea huegelii* (glaucous form)
  - *Grevillea obliquistigma*
  - *Grevillea oncogyne*
  - *Grevillea paradoxa*
  - *Grevillea phillipsiana*
  - *Grevillea teretifolia*
- Proteaceae
  - *Hakea falcata*
  - *Hakea francisiana*
  - *Hakea pendens*
  - *Hakea subsulcata*
  - *Isopogon robusta* ms
  - *Persoonia inconspicua*
  - *Persoonia trinervis*
  - *Petrophile seminuda*
- Rhamnaceae
  - *Cryptandra myriantha*
  - *Stenanthemum stipulosum*
  - *Trymalium myrtillus*
- Rutaceae
  - *Boronia subsessilis*
  - *Drummondita wilsonii*
  - *Microcybe multiflora* var *multiflora*
  - *Phebalium filifolium*
  - *Phebalium megaphyllum* ms
  - *Phebalium tuberculosum*
  - *Phebalium tuberculosum* x *Phebalium megaphyllum* ms
- Santalaceae
  - *Exocarpos aphyllus*
  - *Santalum acuminatum*
- Sapindaceae
  - *Dodonaea amblyophylla*
  - *Dodonaea bursariifolia*
  - *Dodonaea caespitosa*
  - *Dodonaea lobulata*
  - *Dodonaea microzyga* var *acrolobata*
  - *Dodonaea stenozyga*
- Solanaceae
  - *Lycium australe*
- Stylidiaceae
  - *Stylidium limbatum*
- Zygophyllaceae
  - *Tribulus astrocarpus*
  - *Zygophyllum apiculatum*
  - *Zygophyllum glaucum*

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Termites (Isoptera) in Western Australia: present and future directions of ecological research

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Abstract

The present study reviews the extent to which termite abundance and species richness (alpha diversity) has been measured for major vegetation and disturbance types in Western Australia, critically examines sampling methodologies and suggests priorities for future research.

Termite abundance and species richness (at the site level) are best documented for eucalypt woodlands and heath/shrublands, and are least well documented for eucalypt forests, *Banksia* woodland, mallee, mulga woodland/shrubland and hummock grasslands. Of the disturbance effects, most is known about habitat fragmentation, livestock-grazing, regenerated farmland and rehabilitated bauxite mines; least is known about the effects of fire, and termites in cultivated soils or under exotic timber plantations.

Sampling methods vary widely but fall into two major groups. Firstly, termite-only studies used soil-trenching/skimming and hand-collecting from mounds, surface wood, stumps, roots, *etc.* Secondly, broad-based investigations, covering a range of arthropod taxa, used various combinations of soil and litter cores/quadrats and pitfall traps. Most broad-based studies were carried out in eucalypt forests of the south-west, with an emphasis on the effects of fire. No fire study has measured termite species richness, and most broad-based (and all fire) studies were restricted to three or less study sites, with no replication for treatments (*e.g.* burnt-unburnt). Lack of replication makes it difficult to identify treatment effects from natural variation.

Termite species richness has been found to be a valid surrogate for termite abundance (dry biomass) for south-west ecosystems (eucalypt woodland, mallee, shrubland; Abensperg-Traun & De Boer 1990).Termite genus richness has been found to be the most effective surrogate for species richness in rehabilitated minesites (Nichols & Bunn 1980) and jarrah forest (Bunn 1983), but declined in efficiency for more species-rich ecosystems where a small number of genera contribute most species. Mean species-to-genus ratios were 1.08 for jarrah forest and rehabilitated minesites, 1.49 for gimlet (*Eucalyptus salubris*) woodland (Abensperg-Traun *et al.* 1996b), 1.52 for wandoo (*E. capillosa*) woodland (Abensperg-Traun 1992) and 1.66 for shrubland (Abensperg-Traun unpublished).

Sound ecosystem management requires adequate knowledge of spatial patterns of the abundance and diversity of the biota, as well as their role in ecosystem processes. Current ecological knowledge of the Western Australian termite fauna is inadequate in the following areas;

- the effects of fire on termite abundance and species richness in eucalypt forests and hummock grasslands;
- termite abundance and species richness in spatially extensive but poorly-sampled vegetation types - mallee, mulga woodland/shrubland and hummock grasslands;
- the effects of harvester termites on ecosystem properties in arid and semi-arid (pastoral) regions, particularly in the presence of livestock during drought conditions;
- the relationship between the effects of disturbance on termite communities, and ecosystem function; and
- interactions between termites and other components of the invertebrate fauna, particularly with ants as termite predators.

Introduction

Termites are social insects of predominantly tropical and subtropical regions which account for about 75 % of the land surface of Australia, and more than 80 % of Western Australia. Across the continent, these environments support large termite populations and have a high species richness (Matthews 1976; Braithwaite *et al.* 1988; Stafford Smith & Morton 1990; Whitford *et al.* 1992). There are 260 described Australian species, of which 153 species occur in Western Australia (extracted from data given in Watson & Abbey 1993). The species richness of termites in the mediterranean south-west of Western Australia, for example, is unusually high, relative to its latitudinal position, and rivals the richness of tropical termite communities (Abensperg-Traun & Steven 1997).

There are probably few Western Australian environments where termites are not abundant and diverse, indicating their high functional importance such as their contribution to nutrient-cycling processes (Park *et al.* 1994; Lobry de Bruyn & Conacher 1995) and as food for insectivores (Abensperg-Traun 1994). Areas which support low numbers and few species include some of the southern-most areas (south-coastal; Abensperg-Traun & Milewski 1995). Unpublished personal observations also indicate that areas of high soil salinity (*e.g.* natural salt lake basins and secondarily saline areas with high water tables), and those subject to seasonal flooding, support few termites.

The retention of native habitat as functioning ecosystems, with its component biota, is at the core of nature conservation. Effective ecosystem management necessitates a sound understanding of spatial patterns of faunal abundance and diversity (species richness), and the extent to which different kinds of disturbance factors (*e.g.* fire, habitat fragmentation, livestock-grazing) impact on these community parameters.

Most of Western Australia is subjected to one or more types of habitat disturbance at different spatial scales and levels of intensity, and this impacts on various components of the soil and litter fauna, including termites (Abensperg-Traun & Steven 1996; Majer & Beeston 1996). One current controversy, for example, is how the regular use of fire as a management tool for fuel reduction in south-west eucalypt forests/woodlands may affect the native biota (Christensen & Abbott 1989; Abbott & Christensen 1994; Friend 1995; Calver *et al.* 1996). An added complication to resolving disturbance effects is that the abundance as opposed to species richness of subterranean termite populations is notoriously difficult to quantify because of their highly aggregated distribution in the soil matrix (*e.g.* Nutting & Jones 1990; Eggleton & Bignell 1995). This has obvious implications for studies of disturbance effects where termite communities in undisturbed and disturbed environments are compared.

The present study synthesizes current knowledge of Western Australian termite communities. It reviews the extent to which termite abundance and species richness has been measured for major vegetation and disturbance types, and critically examines the sampling methods used. It then suggests priorities for future research.

Methods

All published ecological studies of Western Australian terrestrial arthropod communities were reviewed for termite coverage. Studies that measured termite abundance and/or species richness were examined for the sampling methods and the broad vegetation and disturbance types that were investigated. The major vegetation types considered were *Eucalyptus* forest, *Eucalyptus* woodland, *Banksia* woodland, mallee (*Eucalyptus* spp), mulga (*Acacia aneura*) woodland/shrubland, heath/shrubland and hummock (spinifex) grassland (*Triodia* spp, *Plectrachne* spp). Types of disturbance that I considered were fire, livestock-grazing/trampling, regenerated farmland, rehabilitated minesites, pine plantations, dieback fungus (*Phytophthora cinnamomi*), habitat fragmentation (remnant size and spatial isolation), and termite communities under pasture/wheat-lupin stubble. As a measure of sampling effort for vegetation and disturbance types (across discrete studies), I calculated total numbers of study sites at which termite abundance and/or species richness was assessed. I also examined dimensions of sample units (*e.g.* core width/depth) and numbers of samples collected from study sites. Further, I compared sampling methods used by studies that examined termites only, compared with studies where termites were only one component of a range of soil and litter arthropods investigated, because broad-based studies are likely to use a limited range of methods to cover as wide a range of arthropod groups as possible, resulting in sampling inefficiencies for some taxa. The sampling methods used included soil-trenching/skimming (for details on soil trenching, see Abensperg-Traun & De Boer 1990). This involves intercepting termite foraging galleries and chambers in the top 5 to 10 cm of the soil using a spade and extracting the termites *in situ* by hand. Other sampling methods were soil cores, litter cores (where soil cores incorporated the litter component), litter quadrats, pitfall traps, wooden baits and general hand-sampling where termites were sampled from mounds, dead and decomposed surface wood, roots and stumps, and the leaf litter.

Results

Sampling methods

Studies of termite communities in eucalypt forests used the widest range of sampling methods but never used soil-trenching/skimming; only one study was based on general hand-collections (Bunn 1983). Soil cores, soil and litter cores, and litter quadrats were used most often in eucalypt forests (Table 1). Two studies also used litter quadrats in addition to soil cores, and two studies used pitfall traps only. Soil-trenching/skimming coupled with hand-collections were used most often for eucalypt woodlands and heath/shrublands (Table 1). Only one study (with one study site) used a baiting technique. Most studies used more than one method, and they formed two broad groups; one used soil-trenching/skimming and general hand-sampling, while the second used various combinations of soil and litter cores, litter quadrats and pitfall traps.

With regard to disturbance effects, the widest range of sampling methods was used for the fire studies (Table 1). All work on rehabilitated mine-sites used general hand-sampling only, and the single study of dieback used soil cores and litter quadrats. All other studies used soil-trenching/skimming and general hand-sampling; one study of termites under cultivation used soil cores (Table 1).

In terms of numbers of discrete studies, the effects of fire have been examined more often than any other disturbance factor. When fire studies were further examined for sampling methods and vegetation types, studies in eucalypt woodland, mallee and heath/shrubland vegetation were based almost entirely on data from soil-trenching/skimming and general hand-collecting (Table 2). Fire studies in eucalypt forests, in contrast, were based entirely on data from soil/litter cores, litter quadrats and pitfall-traps (Table 2).

The general pattern for disturbance studies was as for vegetation types; studies that used soil-trenching/skimming and hand-sampling, versus studies that used cores/

Table 1

Numbers of study sites for different sampling methods that were used for the assessment of termite abundance and/or species richness for vegetation and disturbance types. Source of data: Davies (1970); Perry (1972); Abbott *et al.* (1979); Abbott & Parker (1980); Nichols & Bunn (1980); Whelan *et al.* (1980); Bunn (1983); Abbott (1984); Abbott *et al.* (1984); Majer (1984, 1985); Postle *et al.* (1986, 1991); Abensperg-Traun & De Boer (1990); Abensperg-Traun (1992, 1993a); M Burns (1992; School of Environmental Biology, Curtin University, Perth, unpublished report); Little & Friend (1993); Abensperg-Traun & Milewski (1995); Abensperg-Traun & Perry (1995); Abensperg-Traun *et al.* (1993, 1996a,b,c,d).

Vegetation/disturbance	Sampling method						
	Soil trenching/ skimming	Soil cores	Litter cores	Litter quadrats	Pitfall traps	General hand search *	Baiting
Vegetation type							
Eucalyptus forest	0	5	2	3	1	1	0
Eucalyptus woodland	4	1	0	1	1	4	1
Banksia woodland	1	0	0	0	0	1	0
Mulga woodland/shrubland **	1	0	0	0	0	1	0
Heath/shrubland	3	0	0	0	1	3	0
Hummock grassland	1	0	0	0	0	1	0
Disturbance type							
Fire**	2	3	2	2	5	2	0
Livestock-grazing**	2	0	0	0	0	3	0
Regenerated farmland	1	0	0	0	0	1	0
Rehabilitated minesites	0	0	0	0	0	1	0
Pine plantation	1	0	0	0	0	1	0
Dieback	0	1	0	1	0	0	0
Habitat fragmentation	1	0	0	0	0	1	0
Pasture	1	1	0	0	0	1	0

* indicates mounds, standing/lying dead wood, roots, leaf litter, etc; ** indicates inclusion of broad termite survey of Davies (1970) for grazed mulga woodland/shrubland and Perry (1972) for burnt hummock grassland.

Table 2

Numbers of studies on fire effects with regard to sampling methods and vegetation types. See Table 1 for source of data.

Vegetation type	Sampling methods					
	Soil trenching/ skimming	Soil core	Litter core	Litter quadrat	Pitfall-trap	General hand search
Eucalyptus forest	0	3	2	1	2	0
Eucalyptus woodland	2	0	0	1	1	2
Mallee	1	0	0	0	0	1
Heath/shrubland	4	0	0	0	1	4

quadrats/traps. All studies that used soil-trenching/skimming and hand-sampling were termite-only investigations (Table 3). The exceptions were two studies on the effects of habitat fragmentation and recolonization of regenerated farmland where a broad range of soil/litter arthropods were investigated. All other generalized arthropod studies used various combinations of the other methods (cores/quadrats/pitfall-traps).

Sampling effort/regime

When totalling numbers of study sites for vegetation types where termite abundance and/or species richness was measured, eucalypt woodlands and heath/shrublands were sampled most extensively (Table 4). The least work was for termite communities in eucalypt forests, *Banksia* woodland, mulga woodland/shrubland, mallee and hummock grassland. Two broad surveys listed termite species for mulga woodland/shrubland (Davies 1970) and hummock grassland (Perry 1972). Perry *et al.* (1985) listed species for the extreme south-west of the State (coastal and near-coastal forest and woodland ecosystems). There have been no termite community studies for rainforest vegetation in Western Australia.

The greatest number of study sites on disturbance effects were for livestock-grazing, habitat fragmentation, regenerated farmland, rehabilitated bauxite mines and fire (Table 4). The lowest numbers of sites addressed the influence of cultivation and dieback, and the effects of replacing

Table 3

Numbers of studies that used different sampling methods by termite-only studies, and by studies where a broad range of soil and litter arthropods, in addition to termites, were investigated. See Table 1 for source of data.

Sampling method	Type of study	
	Termites only	Broad range of arthropod taxa
Soil trenching/skimming	6	2
General hand search *	7	2
Soil cores	0	6
Litter cores	0	2
Litter quadrats	0	4
Pitfall-traps	0	3
Baits	1	0

* indicates mounds, standing/lying dead wood, roots, leaf litter, *etc.*

native vegetation with exotic, commercial timber such as *Pinus* pine (Table 4). No studies were conducted on the effects of replacing native vegetation with eucalypt plantations.

There was considerable variation between individual studies in the number of study sites, the number of sampling units within sites, and their dimensions (Table 5). There was also wide variation in the number of months/seasons sampled (not shown). However, individual investigators showed some consistency in the number and dimension of their sampling units across different studies (*e.g.* soil cores in studies by Abbott (1984) and Abbott *et al.* (1984); soil trenches in studies by Abensperg-Traun 1992; Abensperg-Traun & De Boer 1990; Abensperg-Traun & Milewski 1994; Abensperg-Traun *et al.* 1996a,b). Diameters of pitfall traps showed least consistency across the different studies. Of 11 discrete studies that used a combination of soil/litter cores, litter quadrats and pitfall-traps, four studies sampled two study sites only. These studies lacked treatment replication because all but one of these investigations compared termite abundance in unburnt and burnt vegetation (eucalypt forest). An additional four studies sampled three sites each of which two studies were on the effects of fire (Table 1, 2 and 5). All studies on fire effects are therefore based on data collected from three or less study sites. A study by Abensperg-Traun (1993a) sampled one site only but used high within-site treatment replications as a test of the efficiency of sampling wood-eating termites with different types of woody baits (Table 5).

Table 4

Total numbers of study sites (across separate investigations) at which termite abundance and/or species richness was assessed for vegetation and disturbance types. Source of data: [a] Abbott (1984); [b] Abbott & Parker (1980); [c] Abbott *et al.* (1984); [d] Abensperg-Traun (1992); [e] Abensperg-Traun (1993a); [f] Abensperg-Traun & De Boer (1990); [g] Abensperg-Traun & Milewski (1995); [h] Abensperg-Traun & Perry (1995); [i] Abensperg-Traun *et al.* (1993); [j] Abensperg-Traun *et al.* (1996a); [k] Abensperg-Traun *et al.* (1996b); [l] Bunn (1983); [m] M Burns (1992; School of Environmental Biology, Curtin University of Technology, Perth, unpublished report); [n] Davies (1970); [o] Little & Friend (1993); [p] Majer (1984); [q] Majer (1985); [r] Nichols & Bunn (1980); [s] Perry (1972); [t] Postle *et al.* (1986); [u] Postle *et al.* (1991); [v] Whelan *et al.* (1980); [w] Nichols *et al.* (1989).

Vegetation/disturbance	Total number of study sites	
	Termite abundance	Termite species richness
Vegetation type		
Eucalyptus forest	20 [aclpqtuv]	12 [l]
Eucalyptus woodland	58 [bdefgk]	53 [defgk]
Banksia woodland	0	11 [hi]
Mallee (*Eucalyptus* spp)	9 [bfg]	8 [fg]
Mulga (*Acacia aneura*) woodland/shrubland [1]	0	[n]
Heath/shrubland [2]	48 [fgio]	45 [fgi]
Hummock grassland [3]	0	[s]
Disturbance type		
Fire [3]	20 [acgopqv]	10 [gs]
Livestock-grazing [1]	35 [dk]	36 [dkn]
Regenerated farmland	27 [j]	27 [j]
Rehabilitated minesites	27 [mr]	27 [mrw]
Pine plantation	0	1 [h]
Dieback	1 [t]	0
Habitat fragmentation	29 [k]	29 [k]
Pasture [4]	4 [b]	2

[1] one broad termite survey by Davies (1970); [2] inclusion of mallee-heath and banksia scrub (from Abensperg-Traun & Milewski 1995); [3] one broad termite survey by Perry (1972); [4] Abensperg-Traun, unpublished.

Table 5

Dimensions of sampling units, numbers of samples per site and numbers of study sites used by individual studies. L = length, W = width/diameter, D = depth. Source of data: [a] Abensperg-Traun (1992); [b] Abensperg-Traun & De Boer (1990); [c] Abensperg-Traun & Milewski (1995); [d] Abensperg-Traun *et al.* (1996a); [e] Abensperg-Traun *et al.* (1996b); [f] Abbott *et al.* (1979); [g] Abbott (1984); [h] Abbott *et al.* (1984); [i] Majer (1984); [j] Postle *et al.* (1986); [k] Postle *et al.* (1991); [l] Majer (1985); [m] Whelan *et al.* (1980); [n] Little & Friend (1993); [o] Abensperg-Traun (1993a). Summary excludes general hand collections from microhabitats (wood, mounds, litter, *etc*).

Sampling units	Dimensions of sampling units (mm)	Number of sampling units per study site	Number of study sites
Soil trenches	1000 (L) x 100 (W) x 100 (D)	20	10 [a]
	1000 (L) x 100 (W) x 100 (D)	20	18 [b]
	1000 (L) x 100 (W) x 100 (D)	20	18 [c]
	1000 (L) x 100 (W) x 100 (D)	20	27 [d]
	1000 (L) x 100 (W) x 100 (D)	20	29 [e]
Soil/litter cores	107 (W) x 53 (D)	8	3 [f]
	106 (W) x 55 (D)	50	2 [g]
	106 (W) x 55 (D)	50	2 [h]
	54 (W) x 97 (D)	10	2 [i]
	54 (W) x 97 (D)	10	2 [j]
	54 (W) x 97 (D)	20	3 [k]
Litter quadrats	190 x 190	10	2 [i]
	190 x 190	10	14 [l]
	190 x 190	10	2 [j]
	190 x 190	20	3 [k]
Pitfall traps	18 (W)	16	3 [m]
	65 (W)	50	2 [g]
	65 (W)	50	2 [h]
	42 (W)	20	14 [l]
	90 (W)	32	3 [n]
	42 (W)	16	27 [d]
	42 (W)	16	29 [l]
Wooden stakes	600 (L) x 50 (W) x 50 (W)	15 *	1 [o]

* indicates 15 replicates each for five wood species.

Discussion

General

Termite research in Western Australia has been biased towards vegetation types in the mediterranean south-west (eucalypt forests and woodlands, heath/shrublands). This bias reflects logistic difficulties of working in remote regions where mulga woodlands/shrublands, mallee and hummock grasslands often predominate. Emphasis on south-west ecosystems, however, ignores the bulk of Western Australia where the functional role of termites (and ants), relative to other taxa, is almost certainly the most important (Matthews 1976; Stafford Smith & Morton 1990).

With the exception of Davies' (1970) broad termite survey on Mileura Station, no study has been conducted on termite communities in the vast pastoral region encompassing most of the arid and semi-arid zone although analogous studies from interstate may provide some insights into termites under pastoral forms of landuse (*e.g.* Watson *et al.* 1973, 1978).

Several investigators have drawn attention to likely sampling deficiencies due to the typically aggregated distribution of termites in soil samples, and their paucity in litter samples and pitfall traps. Examples include .... "no data for a large number of soil cores" (Abbott 1984; Abbott *et al.* 1984); "because of the low numbers and patchy distribution of large soil animals, especially termites, ..., it is unrealistic to examine the statistical significance of differences ..... between virgin and farmed soil" (Abbott & Parker 1980); "numbers of Isoptera (in pitfall traps) were borderline for statistical analysis (Little & Friend 1993); "termites were captured only once in the litter and only occasionally in the soil" (Postle *et al.* 1986). The patchy distribution of termites in cores and litter quadrats was also noted by Majer (1984), and this is widely regarded as one of the major impediments to the effective quantification of the relative abundance of subterranean termite populations (Lee & Wood 1971; Sands 1972; Nutting & Jones 1990; Eggleton & Bignell 1995). Time of year at which termites were sampled may also have influenced sampling deficiencies (see below).

With the possible exception of optimal termite habitat such as some tropical grasslands and savannas, soil cores are rarely effective in quantifying subterranean termite populations, and extracting cores of adequate size (width and depth) are impractical and time consuming (Sands 1972; Eggleton & Bignell 1995). Soil trenches sample a higher soil volume and, although causing higher disturbance to the soil and its biota, they are more likely to provide statistically acceptable data (Kemp 1955; Bigger 1966). For example, the total soil volume sampled by 20 trenches per site in studies by Abensperg-Traun (*e.g.* 1992) was four times greater than the 50 soil cores per site collected by Abbott (1984) and Abbott *et al.* (1984). Soil cores have been used as a primary sampling method in Australian studies, but these were supplemented with additional sampling techniques aimed specifically at termites (*e.g.* Holt *et al.* 1993, 1996). For native earthworms, which also have an aggregated distribution pattern in the soil of jarrah forest, Abbott (1985) found an almost perfect correlation between percent frequency of occurrence and total earthworm density in soil cores ($r^2 = 0.94$). Whether the relationship between abundance/density and frequency of occurrence also holds for the termite fauna remains to be seen. Nevertheless, considerable analytical difficulties (high mean:variance ratio) remain in analyzing termite abundance, even with data from soil trenches (*e.g.* Abensperg-Traun & De Boer 1990). Low efficiency of litter cores/quadrats was shown by the studies of Whelan *et al.* (1980) and Majer (1984, 1985). Pitfall-traps (which can assess harvester termite populations only) may only be used effectively where such termite populations are large, and if trapping coincides with peak harvesting times of the year (James 1991). Harvester termites are particularly prevalent in arid and seasonally arid tropical and sub-tropical regions (*e.g.* Watson & Gay 1970). Frequency of occurrence of termites summed across soil trenches and surface wood/mounds, may also be an inefficient measure of their relative abundance (*e.g.* Abensperg-Traun & Milewski 1995; Abensperg-Traun *et al.* 1996a), unless treatment differences are very considerable (*e.g.* Abensperg-Traun *et al.* 1996b).

When to sample?

The efficiency of soil-based assessments depends not only on the size and density of sample units (cores, trenches) but also on when samples are taken. Termites are highly susceptible to fluctuations in soil moisture and temperature conditions. Studies by Williams (1934) and Abensperg-Traun & De Boer (1990) suggest a minimum soil moisture requirement of about 3.5% to maintain some activity near the surface where most sampling occurs. At higher soil moisture levels, however, soil temperature becomes the determining factor influencing activity (Ueckert *et al.* 1976; Abensperg-Traun & De Boer 1990). Termite biomass near the soil surface in the central wheatbelt of Western Australia, a semi-arid environment with a highly variable climate, declined seasonally (in mid-summer; February) by as much as 95% of its annual peak (in spring; September), largely as a result of heat and drought (Abensperg-Traun & De Boer 1990). Termite species richness in soil trenches was highest following the first good rains in autumn (April) and a rise in soil temperatures in spring; spring and autumn sampling yielded similar species numbers (Abensperg-Traun 1991). Sampling at suboptimal times of the year will exacerbate the effects of termite aggregation in the soil matrix , with a relatively high proportion of samples containing no termites. Ueckert *et al.* (1976) showed that termites migrated to below 124 cm in the soil to avoid soil surface temperatures of less than 10 °C. There is no evidence that different termite species are active at different times of the year. Nevertheless, unless sampling occurs at peak activity periods, surveys should be repeated at several times of the year.

What to measure

Abundance or species richness? Current methods of assessing the relative abundance of subterranean termites are laborious and time-consuming in both the field and laboratory, and are often problematic in terms of mean-to-variance ratios. They are therefore potentially unreliable for comparative purposes (*e.g.* termites in grazed/ungrazed, or burnt/unburnt vegetation). Is there some other (surrogate) measure of termite abundance?

Abensperg-Traun & De Boer (1990) quantified soil-inhabiting termites in the central wheatbelt by extracting all termites from sample trenches (each trench about 5 000 cm^3 of soil) for estimates of biomass and species richness, across 18 study sites and three vegetation types (20 trenches per site, monthly for 11 months). Sites with relatively high mean termite biomass per trench also supported relatively high numbers of soil-inhabiting termite species (Fig 1). Because of a high mean-to-variance ratio, a correlation analysis was unsuccessful in linking biomass with species richness. A positive relationship between abundance and species richness in south-west ecosystems is not peculiar to termites, as might be expected, but applies also to many other invertebrate taxa; earthworms in jarrah forest ($r^2 = 0.42$; Abbott 1985); cockroaches ($r^2 = 0.39$), earwigs ($r^2 = 0.82$) and beetles ($r^2 = 0.62$) in gimlet woodlands (Abensperg-Traun *et al.* 1996b); and ants in rehabilitated minesites ($r^2 = 0.71$; calculated from data in Majer *et al.* 1984). Termite species richness may be a valid surrogate for termite abundance in these particular ecosystems.

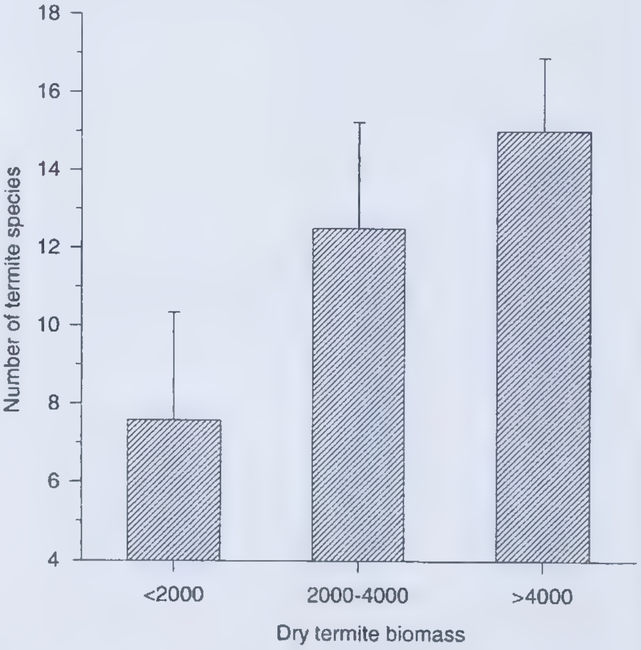

Figure 1. Relationship between termite abundance (mean dry biomass per sample trench per study site, ± sd) and termite species richness in the soil (mean number of species per study site, ± sd) across native habitats in the Western Australian wheatbelt (six study sites each for wandoo *Eucalyptus capillosa* woodland, mallee *Eucalyptus* spp and shrubland; data from Abensperg-Traun & De Boer 1990).

For studies of disturbance effects, species richness may be a more appropriate variable than abundance to measure, because population decline may recover more readily than species loss, particularly in fragmented environments such as the wheatbelt (Abensperg-Traun *et al.* 1996b). Areas of disturbance (*e.g.* bauxite mines and clear-felled coups) nested within eucalypt forests of the south-west may not be constrained by fragmentation effects, however. This is because of adjacent native habitat for recolonization according to island biogeographic theory (MacArthur & Wilson 1967), and Majer *et al.*'s (1984) data on ants in rehabilitated bauxite minesites in south-west forest ecosystems.

Termite species richness is relatively easy to measure and species counts pose no analytical difficulties. However, a sampling regime focused on the soil alone (as in Abensperg-Traun & De Boer 1990) may not effectively sample the resident fauna in terms of species richness. For 27 shrubland sites in the central wheatbelt, for example, soil trenches failed to account for 18 termite species (out of a total of 51 spp; Abensperg-Traun *et al.* 1996a, Table 6), most of which were restricted to dead and decaying wood. Conversely, restricting sampling to wood will not effectively sample the harvester termite component in arid and semi-arid regions in particular, but may provide adequate measures of site richness in south-west forests where harvester termites are scarce (Perry *et al.* 1985). Pitfall traps showed very low efficiency at capturing site richness in wheatbelt habitats (Table 6). This may also apply to more arid and seasonally arid regions where wood-eaters are an important component of the fauna (Saunders 1969; Barrett *et al.* 1973; Watson *et al.* 1978; Braithwaite *et al.* 1988).

Table 6

Sampling effectiveness for assessing termite species richness using three different methods. Data are from 27 shrubland sites in Western Australia's central wheatbelt (Abensperg-Traun *et al.* 1996a,c).

	Pitfall traps	Soil trenches	General hand search *
Species recorded by method	4	28	31
Species not recorded by any other method	0	18	13

* indicates mounds, surface wood, roots, stumps, litter.

Soldier termites are necessary for species identification, so every effort must be made to collect them from each sample. Otherwise, species richness may be significantly underestimated. Some species have very low soldier:worker ratios (Haverty 1977; Abensperg-Traun 1993b). This applies particularly to the predominantly wood-eating *Amitermes* complex which is especially rich in species in shrubland ecosystems of the south-west (Abensperg-Traun & Steven 1997). Perseverence is therefore often required to locate such rare soldiers.

Generic richness? Identifying termites to genus is considerably easier than to species level, and this raises the question whether numbers of termite genera at any one study site effectively describe species numbers also. I examined this relationship for five ecosystem types from the south-west of Western Australia for which the data are adequate. These ecosystems varied in structural and floristic complexity, numbers of study sites, disturbance histories and species and generic richness (Table 7). After log transformation of species and genus numbers, generic richness was significantly correlated with species richness for each of the five ecosystem types (Table 7). Percent variations in species richness explained by genus richness were; wandoo woodland 39 %, shrubland 50 %, gimlet woodland 65 %, jarrah forest 90 % and rehabilitated bauxite minesites 95 %. Not surprisingly, highest percentage variations explained were for ecosystem types with the lowest richness of species and genera (Table 7) because the species-to-genus ratio approached 1. This applied to jarrah forests (mean species-to-genus ratio 1.08) and rehabilitated minesites (mean ratio 1.08). Species-to-genus ratios for other ecosystem types were 1.49 (gimlet

Table 7

Relationships between (log transformed) numbers of termite species and numbers of termite genera for a varying number of study sites across five different ecosystem types in the south-west of Western Australia; r is the correlation coefficient. Source of data: [1] Abensperg-Traun (1992, 1993a); [2] Abensperg-Traun *et al.* (1996b); [3] Abensperg-Traun *et al.* (1996a); [4] Bunn (1983); [5] Nichols & Bunn (1980).

Ecosystem type	Termites Species	Termites Genera	r	Number of study sites
Wandoo (*E. capillosa*) woodland [1]	27	12	0.622*	11
Gimlet (*E. salubris*) woodland [2]	29	12	0.806**	29
Shrubland [3]	58	12	0.706**	27
Jarrah (*E. marginata*) forest [4]	14	10	0.949**	10
Rehabilitated bauxite minesites [5]	10	8	0.974**	20

* $P < 0.05$, ** $P < 0.001$.

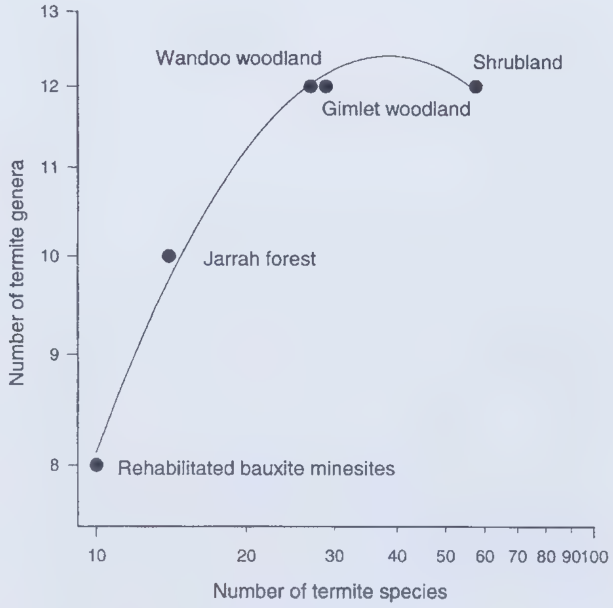

Figure 2. Logistic regression between termite species and genus numbers for five ecosystems types in the south-west of Western Australia (note log-log scale; data from Table 7).

woodland), 1.52 (wandoo woodland) and 1.66 (shrubland). The implication of these ratios is that the use of generic richness as a surrogate for species richness will be unreliable where few genera contribute the majority of species (typically *Amitermes* spp and *Tumulitermes* spp in arid and semi-arid regions). This relationship is consistent with the global pattern for the termites (Eggleton *et al.* 1994), and Australian ants (Andersen 1995). The relationship between total species and genus numbers across the different ecosystem types was highly significant, explaining 99 % of the variation in site richness ($r = 0.996$, $n = 5$, $P < 0.001$; Fig 2).

Future directions

The ecological framework for suggested future termite research in Western Australia emphasizes the broad topics of patterns and processes and focuses on what are considered to be the most important issues.

Patterns. While characteristics of soils (*e.g.* texture, structure) and vegetation (*e.g.* structure, floristic composition) are often cited as major factors influencing termite abundance and diversity (Lee & Wood 1971; Wood & Johnson 1986), most of these observations are unquantified. Given the complexity of many soils (e.g. patchiness of physical/chemical characteristics at all spatial scales) and plant communities (floristic heterogeneity), such as those in the southwest of Western Australia (Lamont *et al.* 1984; McArthur 1991), more detailed data are necessary for a better understanding of spatial patterns. Termite abundance or diversity has also been linked with soil nutrient levels (Ratcliffe *et al.* 1952; Goodland 1965; Ferrar 1982; Wood *et al.* 1982; Salick & Tho 1984; Braithwaite *et al.* 1988; Jones 1990) and microbial biomass of soils (Holt 1996) but causal relationships are acknowledged to remain poorly understood (Holt 1996). Our inadequate knowledge for purposes of ecosystem management extends to spatially extensive but poorly sampled vegetation types where research on the abundance and diversity of termites should be encouraged. They include hummock (spinifex) grassland, mulga woodland/shrubland, mallee and rainforest. Hummock grassland (*Triodia* spp and *Plectrachne* spp), for example, covers more than 50 % of mainland Western Australia (Beard 1969), and mulga (*Acacia aneura*) occupies much of the central third of the State, covering an estimated 700 000 km^2 (Morrisey 1984). Mallee vegetation (*Eucalyptus* spp) covers extensive areas in southern regions (Beard 1990), while rainforest is restricted to small and isolated remnants within a savanna matrix in the northern-most parts of Western Australia (McKenzie *et al.* 1991).

Poor understanding of the major driving forces determining spatial patterns of termite abundance and diversity is matched by our general lack of knowledge of the effects of fire. Given the important role of fire in ecosystem management in Western Australia, this represents one of the most serious short-comings of our current knowledge base. Whether natural or used as a management tool, fire is closely associated with two major Western Australian ecosystem types, eucalypt forests and hummock grasslands (Suijdendorp 1981; Friend 1995). Most eucalypt forests are burnt regularly for fuel reduction (Christensen & Abbott 1989), with rotations of 5 to 6 years for jarrah (*Eucalyptus marginata*), and 7 to 9 years for karri (*E. diversicolor*). For *Triodia pungens* in northern parts of Western Australia, a fire frequency of approximately once every five years has been noted and thousands of square kilometers are often burnt (Winkworth 1967; Suijdendorp 1981; Griffin 1992). Our understanding of fire effects on termite communities in hummock grasslands (for Australia as a whole) is limited to one anecdotal report of the local extinction of *Drepanotermes* harvesters in intensely burnt *Triodia angusta* on Barrow Island (Perry 1972; see also Abensperg-Traun *et al.* 1996c for a discussion of fire effects on the survival of colonies of the harvester termite *Drepanotermes tamminensis*). The only other Australian study on fire effects is an unpublished investigation by Hodda (1992) in tropical Australian savanna ecosystems which has no direct relevance to south-west forests or hummock grasslands in the arid zone.

Processes. The dynamic nature between termites and other elements of the ecosystem, emphasises two process-related issues; those related to habitat modification by termites, and those associated with the interaction between termites and other fauna. We understand reasonably well the extent to which termites modify soils which includes physical disturbance of soil profiles, changes in soil texture, the nature and distribution of organic matter and the distribution of plant nutrients (Holt *et al.* 1980; Park *et al.* 1994; Lobry de Bruyn & Conacher 1995). We also know that termite feeding activities affect plant growth and plant species composition via modification of soil properties (Spain & Okello-Oloya 1985; Spain & McIvor 1988; Andersen & Lonsdale 1990). Following a number of years of above average rainfall and a consequent increase in the availability of plant food, as well as populations of mound-building harvester termites, the combined effects of harvester termites *Drepanotermes perniger* and cattle during a subsequent drought has been linked with the degradation of a mulga (*Acacia aneura*) ecosystem. Increases in mound densities during good years led to almost contiguous areas where the hard pavement-like mound surfaces resisted erosion, plant growth and seedling establishment (Watson & Gay 1970; Watson *et al.* 1973). A subsequent study by Watson *et al.* (1978) suggests a longevity of up to 250 years for the mounds of *D. perniger*. The long-term effects of the combined activities of harvester termites and livestock on arid zone ecosystems are poorly understood yet are of considerable importance for production systems (pastoral industry) as well as ecosystem management for the benefit of native plants and animals.

Conversely, possible flow-on effects on nutrient-cycling and soil formation, for example, following a significant decline in termite abundance and diversity (*e.g.* see Abensperg-Traun *et al.* 1996b) remain unclear. There is a great paucity of empirical evidence linking declines in arthropod abundance and diversity in general, and that of termites in particular, with changes in rates of ecosystem function (Hobbs *et al.* 1995; Naeem *et al.* 1995). There may not be a rectilinear relationship between *e.g.* termite diversity and ecosystem function (*e.g.* rates of nutrient-cycling). The data of Springett (1976), for example, showed an asymptotic (logistic) relationship between the diversity of soil microarthropods and litter decomposition in pine plantations of the south-west of Western Australia. In other words, a minimum number of species may be required for full ecosystem function, while at some threshold additional species add little further function, other than as an insurance policy in times of disturbance and change when a full compliment of species (and their functional characteristics) enhance ecosystem stability (Main 1981). The magnitude of flow-on effects following a loss of termite species and numbers would clearly depend on the severity of the decline, on density compensation by other termite species with comparable functional roles, and on the importance of termites relative to other soil and litter invertebrates. Where termites are high in numbers and species, particularly in arid and semi-arid regions, other macroinvertebrates (except ants) are less well adapted to the prevailing environmental conditions and are therefore comparatively minor components of the fauna in terms of numbers and biomass (Matthews 1976; Stafford Smith & Morton 1990). Here, detrimental flow-on effects on other components of the ecosystem are likely to be of much greater significance than in areas where termites are a minor component (Cushman 1995). However, a significant decline in termite abundance and diversity as a result of disturbance is likely to see a decline in some other groups also (Abensperg-Traun *et al.* 1996b).

Compared to ants which interact intensively with a wide range of other fauna, particularly as predators and competitors (Holldobler & Wilson 1990), termites are timid, cryptic and specialized foragers of plant matter, with comparatively few interactions with other invertebrates. The most apparent interactions involve their role as food for predators and as hosts for other fauna within their nest structures. Here also we have varying levels of ecological insights of the range, nature and intensity of interactions. Predation may occur at varying levels, namely on the nest, on individual foragers or on winged reproductives (alates) during their nuptial flight, involving vertebrates and invertebrates. The availability of termite alates in spring represents a major source of food for insectivores, ensuring the availability of large amounts of fat-laden food items at a time when most insectivores (birds, some mammals, reptiles and frogs) have initiated breeding activity and hence have elevated energy requirements (see also Discussion in Abensperg-Traun 1994). Predation may also occur from within the nest by termitophilous invertebrates (Watson & Gay 1991). Predation on termites by mammals and lizards is much better known than that of the invertebrates, particularly the ants with whom termites are known to have coevolved in an intense predator-prey relationship (see Holldobler & Wilson 1990 on the 'arms race' between termites and ants). In Africa, whose termite fauna resembles the Australian fauna in abundance and diversity, several ant species are termite-specialized (Longhurst *et al.* 1978, 1979), as are other invertebrates such as some spiders (Dippenaar-Schoeman & Meyer 1980; Eberhardt 1991; Jocque & Dippenaar-Schoeman 1992) and possibly several species of land planarians (Jones *et al.* 1990). Some aspects of the interactions between termites and ants in Australia are given by Greenslade (1970), Holt & Greenslade (1979), Higashi & Ito (1989) and Holt (1990), but our understanding of the extent and effects of ant (and other invertebrate) predation on termites deserves more intensive research.

Termite mounds are host to many small mammals, birds, reptiles, frogs and other invertebrates, including termites, using the mounds as shelter, breeding and feeding sites (Mitchell 1965; King & Green 1979; Spain & Brown 1979; Braithwaite 1990). Some mound co-inhabitants (other termites, *e.g. Ahamitermes* spp, termitophilous beetles *Drepanoxenus* spp) have been recorded only from the mounds of particular termite species, suggesting host specificity (Gay 1955; Watson & Kistner 1985; Watson & Gay 1991). Some of these interactions may be more in need of research than others, but all deserve preservation as part of thoughtful and effective ecosystem management.

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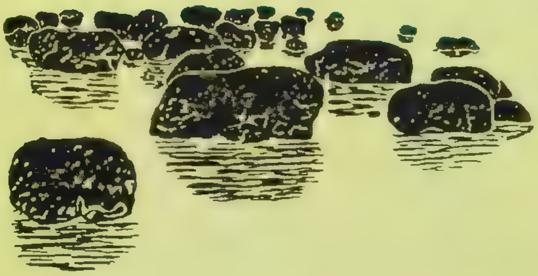

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Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences ambraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

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Long-term sampling of a herpetofaunal assemblage on an isolated urban bushland remnant, Bold Park, Perth

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Abstract

Twenty-nine species of herpetofauna (three frogs, seven snakes and nineteen lizards) were recorded from an isolated urban bushland remnant, Bold Park, Perth. Four habitats were sampled by fenced pitfall trapping for a total of 398 days extending over seven years. There were marked differences in activity patterns of the herpetofauna through the year, with the greatest numbers trapped in November and December. Species trapped first in the sampling regime were also those most frequently captured; several species were not prone to pitfall trapping. Although sampling effort varied between years, in no single year were all 29 species trapped; on average only 79% of the assemblage was captured in any one year. About 100 individuals were captured before 50% of the total assemblage was recorded and around 200 individuals for 80% of the assemblage; this equates to between 360-480 pit-days and over 960 pit-days of trapping effort, respectively. These data have implications for the sampling regimes and analyses of surveys undertaken to document herpetofaunal assemblages for environmental impact assessments, conservation and management plans.

Introduction

The colonisation of Western Australia by Europeans in 1829 commenced a marked and irreversible alienation of natural ecosystems and their composite assemblages of fauna. This transformation of the landscape is profound in Perth, the major urban centre of Western Australia, which now accommodates nearly 1.2 million people and which has few remnants of the original ecosystems.

In 1978 the Western Australian Museum documented the fauna of the northern Swan Coastal Plain to determine, in part, the vertebrate fauna species still extant in the region and to evaluate the impact of the first 150 years of settlement on vertebrates. Some 20 species of mammals and six birds had become locally extinct since settlement (see How & Dell 1993). Further sampling was commenced in 1986 of three isolated bushlands in the inner urban areas of to determine the variation in the fauna across the major landform units and specifically of the *Banksia* woodlands on the Swan Coastal Plain (How & Dell 1989).

Analysis of these surveys and examination of data from several other site-specific faunal surveys showed a marked geographic patterning of the herpetofaunal assemblages on the landforms of the Perth area. This was related to both major landform types and geographic barriers (How & Dell 1994). The caveat that was applied to the data used in that analysis was that sampling had to have encompassed at least 10 days of intensive collection during the spring period. The sampling of the three inner urban bushland remnants, commenced in 1986, continued through until 1990 in two cases and until 1993 in the third. The aim of extending these surveys was to determine the seasonal activity, annual variation and "total" assemblages of the herpetofauna in these remnants. I examine here the first seven years of sampling at Bold Park, the longest sampled of these three remnants, and illustrate the effort expended to adequately document the herpetofaunal assemblage

Methods

Bold Park is a bushland remnant of some 330 ha located close to the Indian Ocean about 10 km west of central Perth. The preliminary list of vertebrate species from Bold Park has already been published (How & Dell 1990).

This herpetofaunal survey of Bold Park was undertaken between December 1986 and June 1993 using four similar fenced pitfall traplines. The fenced pitfall traplines consisted of six pitfall traps placed in a line between 7 and 8 metres apart. Each pit trap consisted of a 17.5 cm diameter PVC pipe that was 60 cm deep and sealed at the bottom with fly-screen mesh. Drift fences that were 50 m long fly-screen mesh, 30 cm high and dug 5 cm into the substrate, crossed each of the 6 pitfall traps. Each pitfall trap open for 24 hours was referred to as a pit-day.

The four habitats selected for surveying represent the principal vegetation types and most of the vegetational heterogeneity of Bold Park determined by Keighery *et al.* (1990). These habitats were;

- BP1 Mixed coastal heath
- BP2 *Dryandra sessilis* shrubland
- BP3 *Banksia attenuata / B. menziesii* low woodland
- BP4 *Eucalyptus gomphocephala* (Tuart) woodland

The first of these sampling sites (BP1) was located on

Table 1

Number of days trapping and the number of individuals trapped for each month of each year between December 1986 and June 1993 at Bold Park. The mean number of individuals trapped daily during each month is also calculated. Twenty four pitfall traps were open each day at Bold Park.

	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	Total
86/87	-	-	-	-	-	4/62	0	4/25	4/17	0	4/13	4/3	20/120
87/88	0	0	5/20	6/38	12/191	6/103	8/49	6/32	6/22	6/17	0	0	55/472
88/89	0	0	6/16	10/33	6/92	14/225	7/56	0	7/45	6/19	0	0	56/486
89/90	0	0	0	25/64	5/52	10/94	10/52	4/14	0	16/82	0	0	70/358
90/91	0	0	0	8/20	17/182	2/30	0	15/56	14/38	0	0	0	56/326
91/92	0	0	0	0	10/115	12/151	7/51	10/47	2/14	0	8/2	0	49/380
92/93	0	0	0	0	27/171	30/277	8/49	14/52	12/30	1/2	0	0	92/581
total	0	0	11/36	49/155	77/803	78/942	40/257	53/226	45/166	29/120	12/15	4/3	398/2723
Ind/day			3.27	3.16	10.43	12.08	6.43	4.26	3.69	4.14	1.25	0.75	6.84
Ind/10pit-days			1.36	1.32	4.35	5.03	2.68	1.78	1.54	1.72	0.52	0.31	2.85

Table 2

Number of individuals of each species recorded in each habitat and during each year of the Bold Park sampling program.

	SITES				TOTAL	YEARS						
	BP1	**BP2**	**BP3**	**BP4**		**86/87**	**87/88**	**88/89**	**89/90**	**90/91**	**91/92**	**92/93**
Trapping Days	**398**	**398**	**398**	**398**	**398**	**20**	**55**	**56**	**70**	**56**	**49**	**92**
Pit-days	**2388**	**2388**	**2388**	**2388**	**9552**	**480**	**1320**	**1344**	**1680**	**1344**	**1176**	**2208**
LEPTODACTYLIDAE												
Heleioporus eyrei	0	34	37	0	71	5	6	8	23	8	7	14
Limnodynastes dorsalis	48	45	40	13	146	5	25	37	50	8	4	17
Myobatrachus gouldii	2	7	11	5	25	0	1	5	10	1	0	8
ELAPIDAE												
Pseudonaja affinis	0	1	0	0	1	0	0	0	1	0	0	0
Simoselaps bertholdi	26	24	52	20	122	6	22	21	10	18	23	22
Simoselaps bimaculatus	3	1	5	1	10	2	3	1	0	0	2	2
Simoselaps calonotos	1	4	8	3	16	1	4	3	5	3	0	0
Simoselaps fasciolatus	4	1	2	0	7	0	2	2	0	3	0	0
Simoselaps semifasciatus	14	2	1	5	22	1	1	6	2	4	2	6
TYPHLOPIDAE												
Ramphotyphlops australis	2	11	10	4	27	0	3	3	2	7	2	10
AGAMIDAE												
Pogona minor	18	2	10	2	32	0	11	3	4	5	5	4
Tympanocryptis adelaidensis	1	16	2	0	19	0	3	9	4	1	0	2
GEKKONIDAE												
Diplodactylus alboguttatus	1	0	0	0	1	0	1	0	0	0	0	0
Diplodactylus spinigerus	39	35	40	0	114	13	41	31	4	6	11	8
PYGOPODIDAE												
Aprasia repens	3	2	0	14	19	0	4	2	1	3	1	8
Lialis burtonis	20	24	36	4	84	2	25	6	7	8	20	16
SCINCIDAE												
Cryptoblepharus plagiocephalus	0	4	3	20	27	3	8	2	5	2	2	5
Ctenotus fallens	226	81	109	47	463	35	83	68	54	63	74	86
Ctenotus lesueurii	48	3	8	0	59	10	13	18	3	3	5	7
Cyclodomorphus celatus	12	0	0	0	12	1	2	4	2	1	1	1
Hemiergis quadrilineata	112	267	334	285	998	11	131	169	114	141	160	274
Lerista elegans	33	40	36	67	176	10	28	30	24	25	21	38
Lerista lineopunctulata	62	38	43	21	164	6	35	20	11	24	29	39
Lerista praepedita	2	6	9	0	17	0	2	2	3	2	1	7
Menetia greyii	4	5	7	24	40	6	7	6	8	8	3	2
Morethia lineoocellata	0	0	1	0	1	0	0	1	0	0	0	0
Morethia obscura	0	0	2	0	2	0	0	0	2	0	0	0
Tiliqua rugosa	15	15	6	7	43	2	10	9	8	6	7	3
VARANIDAE												
Varanus gouldii	2	1	1	0	4	0	1	0	1	1	0	2
Individuals	698	669	813	542	**2722**	120	472	486	358	326	380	581
Species	24	25	25	17	29	18	25	25	25	24	21	23

Table 3

The mean number of captures of species in the various taxonomic categories comprising the entire herpetofaunal assemblage at Bold Park. The mean number of days of trapping to first capture of the species and the mean number of individuals of other species captured prior to first capture of a species are also presented. Means are presented with standard deviation, and sample size in parentheses. Twenty four pit-days occurred on each day of trapping at Bold Park.

TAXON	Captures	Days to first capture	Individuals of other species
Frogs	80.7 ± 61.1(3)	11.3 ± 8.5(3)	81.0 ± 46.9(3)
Snakes	29.3 ± 41.8(7)	41.1 ± 66.0(7)	293.3 ± 487.1(7)
Lizards	120.1 ± 239.3(19)	25.7 ± 36.4(19)	186.1 ± 280.0(19)
Skinks	167.3 ± 293.4(12)	26.2 ± 44.8(12)	203.3 ± 346.1(12)

the sands of the near-coastal Quindalup Dune landform and the remainder (BP2-4) were located on the adjacent and more easterly Cottesloe sands of the Spearwood Dune landform.

Spearman Rank Correlation analysis of the data was undertaken using the Statistix (1996) software package. The species accumulation graphs for species/individuals was undertaken using Microsoft Excel.

Results

Herpetofauna assemblage

A total of 398 days of trapping (2388 pit-days) was undertaken in each of the four habitats resulting in 2722 captures of 29 species during the years 1986 to 1993.

The duration and intensity of trapping varied between years (Table 1). During the first two years of the study, sampling was undertaken for short periods (4-7 days) at regular intervals. This regime indicated that a pronounced activity peak occurred for the majority of the species during the spring-early summer period. Sampling was intensified around this period during subsequent years, but greater effort was also expended in late summer-early autumn when the young of many reptile species hatch and become active.

The 29 species trapped comprised three frogs, six front-fanged snakes, a blind snake, two dragons, two legless lizards, two geckos, 12 skinks and a monitor (Table 2). Several species were infrequently captured by the pitfall trapping regime of the survey. Larger species, such as Gould's monitor (*Varanus gouldii*) and dugite (*Pseudonaja affinis*) were rarely trapped although they were occasionally sited and their tracks were frequently observed. The arboreal marbled gecko (*Phyllodactylus marmoratus*) was frequently observed during nocturnal searches with head-torches, but was not pitfall trapped. The legless lizard *Pletholax gracilis* is known from only six captures made in a floristically rich heath in the centre of Bold Park (Jiang, Kunming Institute of Zoology, pers comm). All traplines were over 500 meters from the nearest freestanding water and it appears that this precluded the capture of several additional species of frog known from the nearby Perry Lakes.

The study extended for nearly 7 years and around 400 trapping days and, since no additional species were trapped for the last 210 days (1336 captures) of trapping, it was assumed that the total assemblage of Bold Park had been recorded.

Species collected earlier during the trapping regime were also those that were most common in the sampled assemblage. This is reflected by the strong negative correlation (Spearman Rank Correlation -0.8304, P < 0.01) between the number of captures of each of the 29 species and the sequence of first capture of that species in the total assemblage.

The average number of captures for each species in each of the various taxonomic categories is presented in Table 3 for the complete assemblage. The average number of days trapping before a species was first captured and the mean number of individuals of other species caught prior to the first capture of a species is also presented. Snakes were less frequently captured than lizards either because they are less abundant or because they are not as prone to capture in pitfall traps.

The effort expended to document the assemblage and the proportion of the assemblage documented after selected effort intervals or individuals trapped is

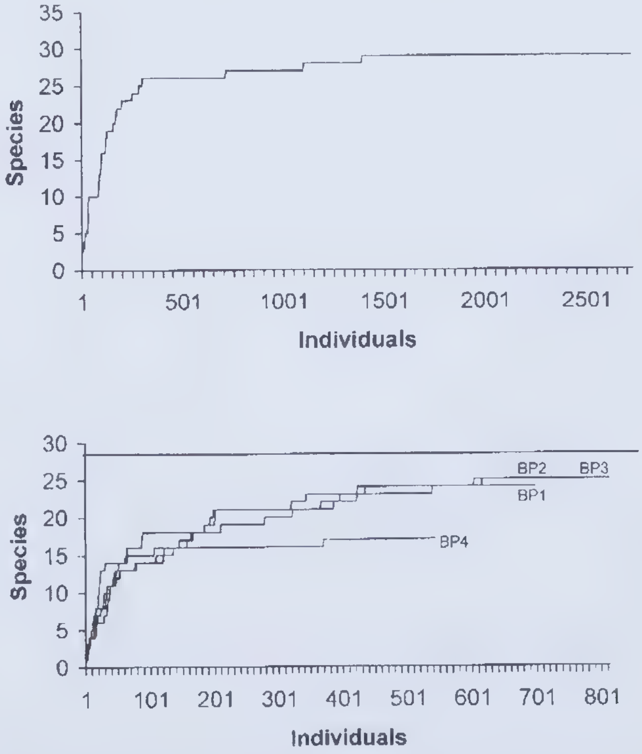

Figure 1. Species accumulation curves for the total herpetofaunal assemblage at Bold Park (top) and the herpetofaunal assemblages of the four habitats (BP1-4) sampled (bottom).

Table 4

The number of species captured at Bold Park after selected intervals of trapping and their percentage of the total assemblage documented. Data are presented for both all herpetofauna and only lizards and using both the number of trapping days and the number of individuals trapped for the assemblages in each habitat as well as all of Bold Park. Six pit-days occurred for every day of trapping in each habitat and 24 pit-days every day for all of Bold Park.

	BP1	BP2	BP3	BP4	Mean % ± SD	Total
HERPETOFAUNA						
Days						
10	7-29%	7-28%	8-32%	7-41%	32.5±5.9	13-45%
20	11-46%	9-36%	9-36%	9-53%	42.8±8.3	18-62%
30	13-54%	14-56%	12-48%	10-59%	54.3±4.7	20-69%
40	16-67%	14-56%	14-56%	13-76%	63.8±9.7	24-83%
50	18-75%	15-60%	16-64%	14-82%	70.3±10.0	26-90%
75	18-75%	16-64%	18-72%	14-82%	73.3±7.5	26-90%
100	21-88%	18-72%	21-88%	16-94%	85.5±9.4	27-93%
150	21-88%	19-76%	22-88%	16-94%	86.5±7.6	28-97%
200	22-92%	21-84%	23-92%	16-94%	90.5±4.4	29-100%
250	24-100%	23-92%	24-96%	16-94%	95.5±3.4	29-100%
Individuals						
25	6-25%	13-52%	8-32%	8-47%	39.0±12.6	5-17%
50	13-54%	14-56%	12-48%	13-77%	58.8±12.6	10-35%
100	18-75%	15-60%	14-56%	14-82%	68.3±12.3	16-55%
150	18-75%	16-64%	17-68%	16-94%	75.3±13.3	19-66%
200	20-83%	18-72%	19-76%	16-94%	81.3±9.6	23-79%
250	21-88%	19-76%	21-84%	16-94%	85.5±7.6	23-79%
300	21-88%	20-80%	21-84%	16-94%	86.5±6.0	25-86%
350	21-88%	21-84%	22-88%	16-94%	88.5±4.1	26-90%
400	23-96%	22-88%	23-92%	17-100%	94.0±5.2	26-90%
Total spp	**24**	**25**	**25**	**17**		**29**
LIZARDS						
Days						
10	6-38%	6-40%	6-38%	5-50%	41.5±5.8	10-53%
20	8-50%	6-40%	6-38%	6-60%	47.0±10.1	11-58%
30	10-63%	9-60%	8-50%	7-70%	60.8±8.3	12-63%
40	13-81%	9-60%	9-56%	9-90%	71.8±16.4	15-80%
50	14-88%	10-67%	10-63%	9-90%	77.0±14.0	17-90%
75	14-88%	11-73%	11-69%	9-90%	80.0±10.6	17-90%
100	15-94%	13-87%	13-81%	9-90%	88.0±5.5	18-95%
150	15-94%	13-87%	14-88%	9-90%	89.7±3.1	19-100%
200	15-94%	14-93%	15-94%	9-90%	92.8±1.9	19-100%
250	16-100%	14-93%	16-100%	9-90%	95.8±5.1	19-100%
Individuals						
25	5-31%	9-60%	6-38%	6-60%	47.3±15.0	5-26%
50	10-63%	9-60%	8-50%	9-90%	67.8±17.1	8-42%
100	14-88%	10-67%	9-56%	9-90%	75.3±16.5	11-58%
150	14-88%	10-67%	10-63%	9-90%	77.0±14.0	12-63%
200	15-94%	12-80%	11-69%	9-90%	83.3±11.2	14-74%
250	15-94%	12-80%	13-81%	9-90%	86.3±6.9	14-74%
300	15-94%	13-87%	13-81%	9-90%	86.3±6.9	16-84%
350	15-94%	13-87%	15-94%	9-90%	91.3±3.4	17-90%
400	15-94%	13-87%	15-94%	9-90%	91.3±3.4	17-90%
Total spp	**16**	**15**	**16**	**10**		**19**

presented in the final column of Table 4. These data indicate that around 100 individuals need to be captured before 50% of the total assemblage is documented while around 200 individuals are needed to document 80% of the assemblage. This translates to between 360-480 pit-days for 50% of the assemblage to be recorded and around 960 pit-days for 80% of the assemblage to be recorded.

When only the lizard assemblage is considered, 80% of the species are documented between 250 and 300 captures or around 960 pit-days of trapping. The species accumulation graphs for the total assemblage and the assemblages in each habitat are plotted in Fig 1.

Variation between habitats

Distinct habitat preferences were exhibited by many

Table 5

The percentage of the total herpetofaunal assemblage of 29 species trapped after successive 10-day intervals during each of the seven years of the Bold Park trapping study. Mean and standard deviation for the respective time intervals are also presented.

DAYS	86/87	87/88	88/89	89/90	90/91	91/92	92/93	Mean
10	44.8	51.7	31.0	37.9	34.5	51.7	48.3	42.8 ± 8.4
20	62.1	75.9	65.5	51.7	58.6	58.6	65.5	62.6 ± 7.6
30	-	82.8	79.3	65.5	72.4	69.0	65.5	72.4 ± 7.3
40	-	86.2	86.2	75.9	79.3	72.4	69.0	78.2 ± 7.1
50	-	86.2	86.2	79.3	82.8	72.4	75.9	80.5 ± 5.6

of the species. Only 15 of the 29 species (52%) were captured in all four habitats surveyed at Bold Park (Table 2).

Species such as the gecko *Diplodactylus alboguttatus*, and the skinks *Morethia lineoocellata*, *M. obscura* and *Cyclodomorphus celatus*, are uncommon in Bold Park, with both a restricted habitat preference and low abundance. Dugites (*Pseudonaja affinis*), although captured in only one habitat, occurred throughout the Park and the tracks of large adults were recorded in every habitat. A yearling was captured in the pitfall traps. The Tuart woodland (BP4) site was considerably less species rich than were the other three sites, principally due to the absence of 5 species of skinks.

No new species were added to the assemblage lists of the habitats for the last 174 days of trapping for BP1, 51 days for BP2, 91 days for BP3 and 139 days for BP4. This equated to 274, 65, 197 and 172 captures, respectively. In each of these habitats six pitfall traps were operated each day.

For the assemblages recorded in each of the four habitats the correlation between the number of individuals of each of the 91 species populations documented and their capture sequence was strongly negative (Spearman Rank Correlation -0.8274, $P < 0.01$) again indicating that the more common species are trapped first.

Although 54% of the assemblage was usually documented by day 30 (180 pit-days), between 75 and 100 trapping days (450 - 600 pit-days) were needed to document 80% of the herpetofaunal assemblage in each habitat (Table 4). On average, nearly 60% of the herpetofaunal assemblages in habitats were documented after 50 captures, while 80% of the assemblages were documented before 200 captures. For just the lizard assemblages of the four habitats, the average effort needed to record 80% of the assemblage was 150-200 captures or 75 days.

Variation Between Years

Over the seven years there was pronounced variation in the assemblages recorded for Bold Park (Table 2). The number of species documented varied from 18 in 1986/1987 (only 20 trapping days) to 25 for the year's 1987/1988, 1988/1989, and 1989/1990. Fewer species were trapped in 1992/1993 when trapping effort was far greater (see Table 1) and focussed on the peak activity period of November -December. The mean percentage of the herpetofauna documented during a year was 79.31 ± 0.09(7) percent (Table 2).

There were extended periods of time between captures for some species in Bold Park, with over three years occurring between retrapping *Simoselaps bimaculatus* in the middle of the study, while *S. calonotos* and *S. fasciolatus* were not retrapped in the last 28 months of the study. These long absences from the trap record impact on the annual documentation of the herpetofauna assemblage as do the limited captures of uncommon or restricted species in Bold Park, such as *Diplodactylus alboguttatus*, *Morethia lineoocellata* and *M. obscura*.

During the six years when trapping effort extended near or over 50 days, the average percentage of the herpetofauna community recorded was only around 80% (Table 5).

Discussion

This long-term survey of the herpetofauna of an isolated bushland remnant in Perth has indicated that a significant effort is required to adequately document the diverse assemblage that exists.

A period of peak activity occurs amongst the herpetofauna during November- December with reduced activity either side of this period and much reduced activity between late-autumn and early spring (Table 1). James (1994) has documented strong seasonal patterns of activity centred on the spring period previously for herpetofauna assemblages in his extensive examination of a central Australian lizard assemblage. He also reported recording 91% and 86% of the lizard assemblage during successive spring census periods.

The reptile assemblage recorded by fenced pitfall trapping at Woodstock Station in the Pilbara (How *et al.* 1991) was 39 species. That survey, which extended over 58 days of pitfall trapping, nine trapping periods, three years and eight discrete habitats, revealed that 25 trapping days (1002 pit-days) elapsed before 80% of the pitfall trapped assemblage was recorded. However, the assemblage revealed by pitfall trapping represented only 58% of the 67 reptile species recorded by all means during the survey (How *et al.* 1991). In a recent survey of the lizard and snake fauna in arid Western Australia, Thompson (1996) recorded most of the 31 species of lizard and eight species of snakes in the first 10 days of trapping, while James (1994) had captured 32 lizard species (82%) after 30 days of trapping, 36 species (92%) after 61 days and all 39 after 180 days in central Australia. These returns for effort are considerably higher than that recorded for the lizard assemblage or even the entire herpetofaunal assemblage documented during the present study in Bold Park where 80% of the total assemblage was recorded only after 40 days (960 pit-days) of trapping. For specific habitats in Bold Park the mean effort expended to record 80% of the assemblage was over 75 days (450 pit-days) for both the herpetofauna and the lizards (Table 4).

This survey has shown that the widespread and common species are also the first captured in the trapping sequence. Uncommon species with restricted habitat preferences are usually the focus of conservation and management programs; such species are generally captured later in the trapping sequence and will probably be missed by short term or low intensity surveys.

Government agencies responsible for auditing the environmental impacts of major developmental projects on faunal communities and assemblages provide guidelines to developers, which are invariably vague and usually stated in broad generalities. If faunal surveys are undertaken, these are generally of short duration and superficial, accounting for little of the annual and seasonal variation inherent in faunal activity. There are few data or long-term studies that assess procedures and methodology for documenting faunal assemblages (Anon 1984; Myers *et al.* 1984); consequently, the potential impact of developments on faunal populations and assemblages cannot be adequately assessed.

The principal finding of this study is that an extensive sampling effort is required in both temporal and spatial scales before the composition of an herpetofaunal assemblage (including its rarer species) can be adequately determined. This knowledge is essential to the proper evaluation of environmental impact statements and for species conservation and management plans.

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The mating biology of *Phasmodes ranatriformis* (Orthoptera: Tettigoniidae: Phasmodinae), a mute genus of bushcricket from Western Australia.

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Abstract

Phasmodes ranatriformis Westwood (Orthoptera: Tettigoniidae: Phasmodinae) is an unusual genus where species are both mute and deaf to airborne sound. As its genus name implies, it resembles certain Phasmatodea in being stick-like. The insect is sexually dimorphic in size; males are much smaller than females. The spring-active species is a pollen and nectar feeder. Census data indicate that there is no bias in the sex ratio while males are more vagile than females as the season progresses. Mating occurs during late spring. There is no evidence of inter-sexual signalling. Females are attracted to food sources at which males also feed and at which mating occurs.

Males produce a spermatophore comprising less that 6% of their body weight. Females do not feed on the spermatophore, which is simply held beneath the subgenital plate. Laboratory studies of mating behaviour show male competition for receptive females. Male-male behaviour ranges from complete disinterest to active jousting for mating opportunities. Prior to copulation the male grasps the female with the abdominal cerci at any point on the female's abdomen, eventually making contact with the genitalia by moving the cerci to the female's terminalia. The male then grasps the ovipositor between its mandibles, maintaining a wheel-like position until the spermatophore is transferred. Females may remate within 24 h. There is a correlation between male size and spermatophore size, and a positive correlation between spermatophore size and time since the previous mating. Males may take as long as 7 days for the spermatophore to reach maximum weight. Males attempting to mate with recently mated females transfer a small fraction (< 1.5 %) of their body weight as spermatophore. Females lay eggs into the soil soon after mating.

Introduction

Males of most tettigoniid insects use acoustic signals to advertise their readiness to mate and receptive females locate calling males by orienting to the source of the sound (Otte 1977; Bailey 1991). The song is also used by males to compete for resources such as calling sites, food or preferred female oviposition sites (Feaver 1983). In those unusual bushcricket species where males are almost deaf, mating strategies have evolved whereby females use spatially discrete food sources as rendezvous sites (Gwynne & Bailey 1988), and males use their calls to solicit matings at these sites (Simmons & Bailey 1990). For example male *Kawanaphila nartee*, a small stick- like species of Zaprochilinae tettigoniid, have significantly reduced hearing function (Bailey & Römer 1991; Bailey & Simmons 1991), and males congregate around flowers rich in pollen and nectar, signalling their willingness to mate to feeding females (Gwynne & Bailey 1988). In *K. nartee*, females, unlike males, are able to detect airborne signals over many meters.

This paper describes the mating behaviour of *Phasmodes ranatriformis*, a nocturnal tettigoniid belonging to the Australian endemic subfamily Phasmodinae (Rentz 1993). The males have no means of sound production, and in both sexes the hearing system is severely reduced. Physiological experiments identified substrate vibration as the most likely means of distance communication in this species (Lakes-Harlen *et al.* 1991), but the sensitivity of the vibration-sensitive subgenual organs was no more developed than in other bushcrickets (*cf* Kalmring & Kuhne 1980). Hence, although substrate-borne vibration may have a role in sexual communication, a more likely way the sexes meet is for males to remain on, and meet with females at feeding sites. Such a system is remarkably similar to that observed for Phasmatodea stick insects (Sivinski 1983).

While plant food may be an important determinant of mating strategy in some bushcrickets, in others the male's donation of a protein-rich spermatophylax is also of importance (Gwynne 1988). The spermatophylax is a glutinous secretion of the male accessory glands and is attached to the externally placed sperm-carrying ampulla. Its size has a profound influence on both male and female mating behaviour (Gwynne 1986, 1988). After copulation females eat the spermatophylax as a nutritious nuptial gift with nutrients contributing directly to the developing eggs (Gwynne 1986). In the absence of the spermatophylax the female will eat the sperm ampula, and so the role of the spermatophylax can also be viewed as a device to protect the male's sperm (Wedell & Arak 1989). A second consequence of the male providing a large and energetically costly spermatophore (Simmons 1990) each time it mates is that the refractory period between successive matings may be over several days, allowing the male to replenish the accessory glands (Davies & Dadour 1989; Simmons & Gwynne 1991).

This paper describes an unusual mating system where the male donates a small spermatophore, which is not fed on directly by the female; the female gains nutrients solely from plants. There is an absence of long distance acoustic communication and mating appears to take place at rendezvous sites. We investigate plant associations of both sexes of *P. ranatriformis* with the hypothesis that mating should occur close to those plants providing most food for the female. If mating is resourced-based then we would expect males to aggregate at and compete for resources used by females, particularly during those periods in the flowering season when the resource is limited. We examine this hypothesis and describe the insect's movement patterns during the season.

Finally, metabolic costs to male tettigoniids of mating are both calling (Bailey *et al.* 1993) and the production of the nutrient rich spermatophore (Simmons 1990). We predict that in mating systems where males are silent and provide very small spermatophores both sexes will re-mate over a relatively short time interval (hours), and competition between males for access to females will be low compared with species where male mating costs are high.

Material and Methods

Field Site

Field studies were conducted during the spring (August - October) of 1992 after preliminary studies during 1990-1991. The study site was an area of 5 hectares in the south-western part of King's Park (Perth), a large city reserve of near natural bush-land. The woodland is dominated by an upper story of *Acacia*, *Banksia* and eucalypts and has a diverse herbaceous layer. The plant community consisted of grass, sedges and herbs (Table 1), which for most of this study contained species in flower. Sources of pollen and nectar from these flowers became less abundant as the season developed (Simmons & Bailey 1990; Gwynne & Simmons 1990).

Table 1

Insect plant association of *Phasmodes rantriformis* in Kings Park ranked by total and for each sex for spring season 1992.

Plant Species		Association	
Perennials	males	females	total
Anigozanthos manglesii	59	44	103
Mesomelaena stygia	14	8	22
Daviesia sp	12	8	20
Xanthorrhoea preissii	9	7	16
Jacksonia sternbergiana	8	7	15
Gompholobium tomentosum	5	6	11
Grasses	6	4	10
Sowerbaea laxiflora	2	7	9
Haemodorum sp	1	1	2
Burchardia umbellata	2	0	2
Gladiolus caryophyllaceus	0	2	2
Banksia attenuata	2	0	2
Casuarina sp	1	1	2
Jacksonia furcellata	1	0	1
Conostylis aculeata	0	1	1
Hibbertia huegelii	1	0	1
Acacia pulchella	1	0	1

The study area selected was known from earlier surveys to have a significant population of *P. ranatriformis* and, during late August to mid-September, is dominated by stands of kangaroo paws (*Anigozanthos manglesii*). This plant provides an abundant source of pollen on which *P. ranatriformis* and *K. nartee* feed (Gwynne & Bailey 1988).

The bushcricket *Phasmodes ranatriformis*

The subfamily Phasmodinae is a sister group to the Zaprochilinae, which have recently been considered a separate subfamily (Gorochov 1988: Rentz 1993). From its highly modified body form and extreme reduction in the acoustic/vibratory mechanism of communication, the insect appears to have evolved independently of other tettigoniid groups, and so the traits that make it so distinctive may be considered derived. Species of this genus, as well as exhibiting the elongate appearance of Phasmatodea stick insects (length 100-200 mm, width 5-10 mm), also show extreme size dimorphism with adult males one third to half the body mass of females.

P. ranatriformis (Fig 1) is entirely phytophagous and as a juvenile will feed on a range of grasses and herbs, but in its pre-adult and adult stages it feeds more exclusively on pollen and nectar. Its appetite for pollen leads to the unusual behaviour of feeding on the perianths of immature, unopened kangaroo paws (*Anigozanthos manglesii*) to attack the newly developed anthers within (Hopper 1993).

Oviposition was observed in sandy soil close to plants and occurred throughout the observation period. Oviposition was twice seen to follow mating, while on another occasion a female was found ovipositing at 1935 h and then with a spermatophore at 2100 h.

Population census

Insects were located by flash-light during the first four hours after sunset by walking randomly through the study area. Searches were repeated every 2-4 days throughout the season. Once found, insects were marked by a numbered tag (3M™ high density reflecting tape - grade 7810). The small, self adhesive tag was fixed to the hind femur. Subsequent re-captures were made easy by this light-reflecting strip, which could be seen over distances exceeding 20 m. The location of each insect was marked with a coloured flagging tape tied to the closest plant, and the distance moved by each insect from its previous site was measured on the following day. Plant associations and the insect's behaviour were noted at the time of capture.

Behavioural observations in the field were made under dim red light. Where interactions occurred with other conspecifics the behaviour was aurally recorded on a cassette recorder and later transcribed. Individuals were allowed to complete their behaviour until the observer was satisfied that any interaction, mating or oviposition behaviour had concluded. Unmarked individuals involved in such an interaction were then caught, marked and released close to the point of capture.

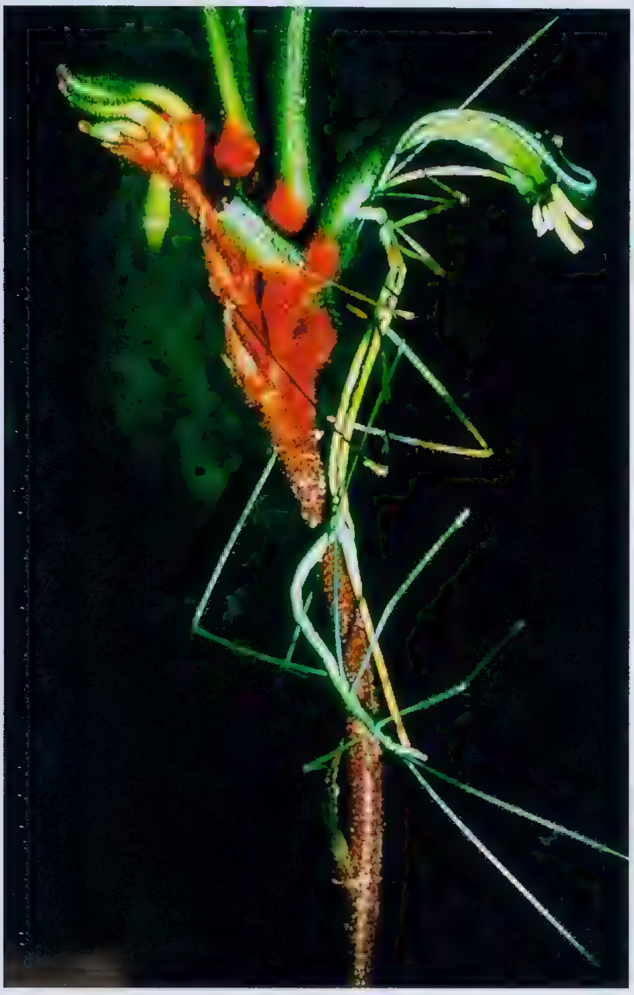

Figure 1. *Phasmodes ranatriformis* mating on a kangaroo paw in Kings Park (photograph by DT Gwynne)

The area of more-or-less homogeneous bushland was bounded by paths, which conveniently delineated our study site. However, once each week we would survey an area 50 m outside this defined site, searching for reflecting tags and so recording the number of emigres.

Laboratory observations of mating behaviour

Males and females were collected during the early adult season (August to early September) as final instar nymphs or recently emerged adults. Field sites used to collect insects for the laboratory were from areas in Kings Park more than 100 m beyond the boundary of the field site described above. Once in the laboratory, insects were housed in a light-reversed regime maintained at 20 ± 2 °C. All individuals were uniquely marked with white liquid correction fluid and placed in large mesh cages with flowers, herbs and pollen *ad libitum*. The weights of each individual were recorded, and for males, weights were taken before and after mating, so giving the weight of the spermatophore passed.

We observed mating in two ways. First, we released two females with a single male (preliminary observations showed that two females placed with a single male increased mating frequency) in a wire-mesh cage (30 cm^3) in which there was fresh vegetation and pollen bearing flowers. Each cage of three insects was observed over the first three hours after darkness. When a female mated she was replaced with another un-mated female. Times to the commencement of mating from the start of the dark period, copulation duration and the number of mating attempts were observed on each occasion. Interactions, whether they resulted in mating or rejection, were noted.

The second approach was to release 8 to 10 males with a similar number of females into larger wire-mesh cages (60 cm^3). This high density arrangement allowed females to exert a choice between males, and for males to compete for mating opportunities. As indicated above, aggregations of both sexes occur in the field, and although not to the same extent as this laboratory manipulation, the situation could have similarities to that found in nature. Again, at the end of each mating, males were temporarily removed and weighed and females, once mated, were allowed to oviposit in sand trays from which eggs were removed.

Results and Discussion

Field Observations

Plant association. During the day *P. ranatriformis* is extremely cryptic, resting along the length of thin leaved plants such as sedges, grasses and the spiny forms of *Jacksonia*. At night the insect may be seen moving over vegetation or feeding on pollen rich flowers. Both sexes are opportunistic feeders, moving from one plant to another as each senesces. In early spring kangaroo paws (*Anigozanthos manglesii)* are a rich source of nutrients and there appears to be a distinct association between these plants and the distribution of *P. ranatriformis* (Table 1). Later in the season, when grass trees (*Xanthorrhoea preissii)* produce their pungently rich nectar, *P. ranatriformis* may be found feeding on flower spikes along with other tettigoniids such as *Kawanaphila nartee* (Simmons & Bailey 1990).

Individual movement. Fig 2 shows the mean distance

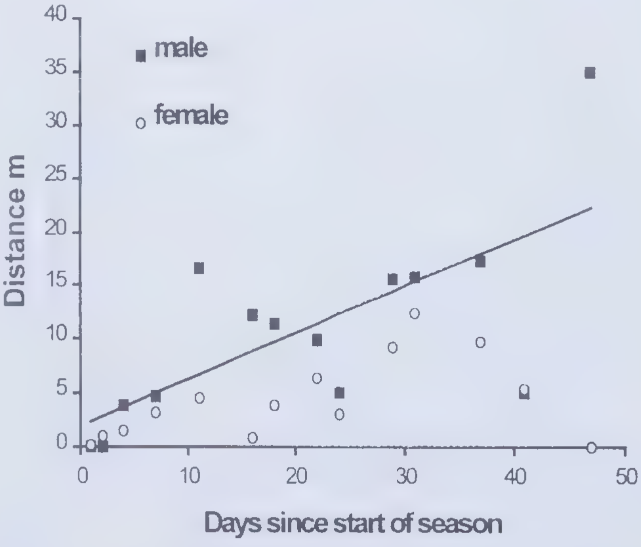

Figure 2. Mean distance moved by both sexes between successive captures over the entire season.

moved by both sexes between successive captures in the field over the entire sampling period. Males increase the distance over which they move as the season progresses ($r^2 = 0.49$; $F_{1,12} = 11.5$; $P = 0.005$), while females showed no significant change in distance moved over the same period ($r^2 = 0.21$; $F_{1,12} = 3.2$; $P > 0.05$). Although most animals moved less than 10 m from the site at which they were first collected, 9 individuals moved over 20 m, and this number included two males moving over 40 m.

Shelly & Bailey (1992) found that female abundance of *Kawanaphilla nartee* was more sensitive to the availability of pollen bearing flowers than male abundance. As flowers senesced females moved out of the sampling area at a great rate than males, presumably because females required higher levels of nutrients to nurture their developing eggs. By contrast, *P. ranatriformis* males rather than females emigrated from sampling areas at a faster rate than males. Increased male movement with the decline in flower availability in *P. ranatriformis,* which is a different measure to emigration, may be related to a reduction in pollen availability and quality. Alternatively, females, once mated, may have been less inclined to mate again and so males would have to move further to find receptive females.

A weekly census of a 20 m strip surrounding the study site showed a low recapture rate (4 males from 117 marked insects of both sexes). We conclude that few animals had emigrated from the study site. An indirect measure of predation was the presence of tags on the ground, which, because of their reflecting quality, could be found at night. These tags could have signified death by predation, the shedding of a limb or merely that the tag fell off. There was no indication of sex biased mortality; 24 tags were recovered of which 11 were from males and 13 from females.

Mating and oviposition. We observed only 7 copulations in the field, and an additional 3 cases where the female was carrying a spermatophore. Nine of these 10 observations occurred before mid-October, and 9 of the 10 after 2000 h. If mating takes place at a rendezvous site then we would expect more than one insect to be present at these sites and, if there was competition for females at the mating site, then a male-biased sex ratio. Two or more individuals were found within 1 m of each other during the time when most matings occurred (Fig 3) but the sex ratio of these small groups of three or more individuals was no different from 1:1.

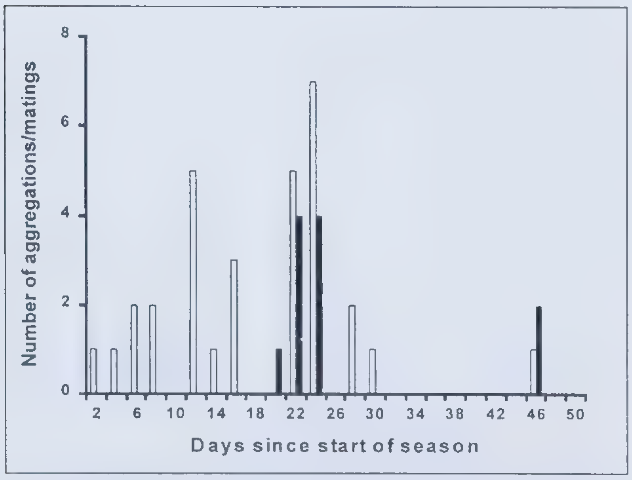

Figure 3. Frequency of aggregations (open) formed from two or more *P. ranatriformis* and number of matings (solid) observed in the field throughout one season.

Laboratory Observations

Male agonistic behaviour. Aggression is a typical part of male behaviour in bushcrickets, particularly where males compete for territory or for mating opportunities (e.g. Feaver 1983). Although we saw no evidence of male agonistic behaviour in the field, in the laboratory males were observed to interact (i) without the presence of a female, (ii) over the possession of females, and (iii) with other males involved in copulation. The frequency and stereotypy of this behaviour suggests that it is part of the male's normal behavioural repertoire and not an artefact of caged insects.

Courtship and copulation. We observed over 50 interactions within both the smaller cages containing 3 individuals (1 male and 2 females), and in larger cages housing 8 to 10 individuals of each sex. Twelve from the 19 copulations took place within 1 hour of scotophase.

Males appeared to detect females when they were within 15-20 cm and walked towards them, occasionally stopping and re-orienting toward her. However, during these occasions there was no evidence of signalling, either by posture or by rhythmic movements of the body or body parts. Once antennal contact was established, the female would either remain passive or walk away. We observed on 8 occasions males and females walking over each other with no apparent indication of their detecting either's presence.

By contrast, males intent on copulation, and once within contact of the female, moved rapidly toward the female with abdomen curved and genitalia open. Successful mating was always preceded by the male grasping the female's long ovipositor with the mandibles, while at the same time curling the abdomen to clasp the female's abdomen. The shortest pre-copulation period saw a male link directly with the female genitalia within 3 s of antennal contact. More usually the male clasped the female's abdomen, and whilst holding on to the ovipositor, could be seen sliding the genitalia toward the genital plate, releasing and re-clasping the abdomen without losing hold of the ovipositor. Once in contact with the female genitalia, the male manoeuvred the female's sub-genital plate before producing a spermatophore. Males remained looped for 5-10 minutes before changing grip on the ovipositor, moving their hold towards its tip. In the field both sexes walked during copulation, often covering distances exceeding 1 m. Once disengaged they broke up with kicking from both sexes.

On no occasion did we observe females feeding on the spermatophore, which was almost entirely hidden by the sub-genital plate. The spermatophore remained visible under the sub-genital plate for approximately 3 h after which time it was absorbed by the female.

Female rejection is a distinct behaviour. After the male makes contact with the female, and begins to loop the

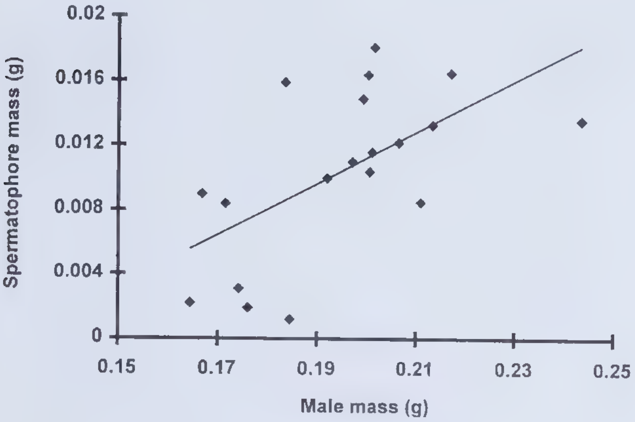

Figure 4. Relationship between spermatophore mass and male body weight.

abdomen towards the wheel position, the female may struggle and kick the male away. On occasions the female lets go of the substrate, dropping to the ground. If the male manages to grasp the female near the genital plate the female will loop around and bite the male until he releases her. Where the female is entirely passive, the male may grasp the female's head, thorax or legs in its unsuccessful attempt at copulation.

Spermatophore size. Spermatophore mass ranged from 0.65-8.98 percent of the male's body weight ($\bar{x} = 5.24 \pm$ se 0.58; n = 19) and had a linear relationship with male weight (Figure 4; $r^2 = 0.37$; $F_{1,18} = 9.8$; $P = 0.0062$). There was no significant relationship between spermatophore size and copulation duration. Some males (n = 4) mated more than once within 24 h but there was no evidence of any relationship between male weight and the number of times the male mated. The replenishment of the spermatophore, expressed by spermatophore mass donated at the next copulation was positively related with the number of days since the previous mating (Fig 5; $r^2 = 0.73$; $F_{1,7} = 16.0$; $P = 0.007$). It would appear that males mated with less than the maximum spermatophore size. Such a finding is consistent with other studies on variation in spermatophore weight with the length of time since the previous mating (Simmons *et al.* 1994).

Repeated mating and male size advantage. Females are polyandrous, and in 4 of 6 cases where a female re-mated within 24 hours, in 3 cases the second male transferred a relatively small portion of the spermatophore amounting to less than < 1.5 % body weight. The fourth case, where the second male's spermatophore was more than 1.5 % of body weight, the first male's spermatophore was close to the mean size. In one case, a recently-mated female allowed a second male to couple, but within a few seconds the second male withdrew and walked away. The minimum time between copulations by a female was 150 mins. Data on repeated copulations (Fig 6), although derived from a small sample size (n = 6) indicate that the second male may be able to detect the presence of the first male's spermatophore, so providing a small spermatophore. In 5 of the 6 occasions where different males mated with an already mated female within 24 hours the second male's spermatophore was smaller and on three occasions was minute.

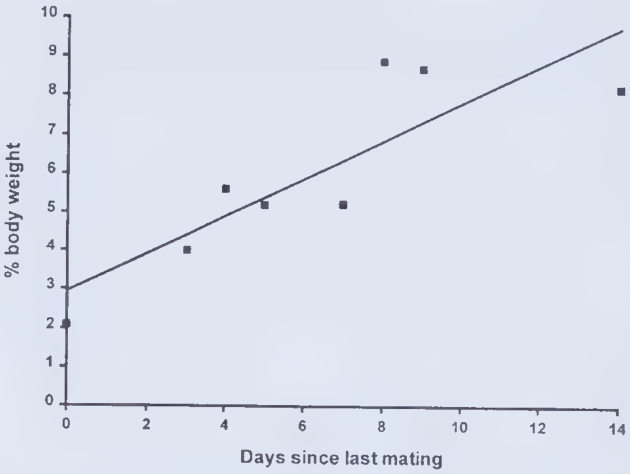

Figure 5. Variation in spermatophore weight, expressed as a percent of male body weight with the time since males last mated.

Of the 49 encounters where both sexes were present *ad libitum* in each cage, larger males gained more mates than smaller males ($t_{45} = 1.78$; n = 49; $P < 0.05$). Thirteen of the 17 males mated and 2 of the rejected males that encountered other females were rejected, each on 6 occasions. These males never mated.

Duration of copulation and refractory period

For many insects, longer copulation confers an advantage to the male, particularly where females are able to re-mate with competing males (Thornhill & Alcock 1983), a case clearly demonstrated by phasmids (Sivinski 1983). But, any adaptive advantage of protracted copulation is more difficult to argue where the male delivers a spermatophore from which the sperm migrate to the spermatheca at a later stage. In most Ensifera, sperm transfer takes place after spermatophore attachment. In this case, increased duration of copulation can only be seen to be an advantage if the presence of the

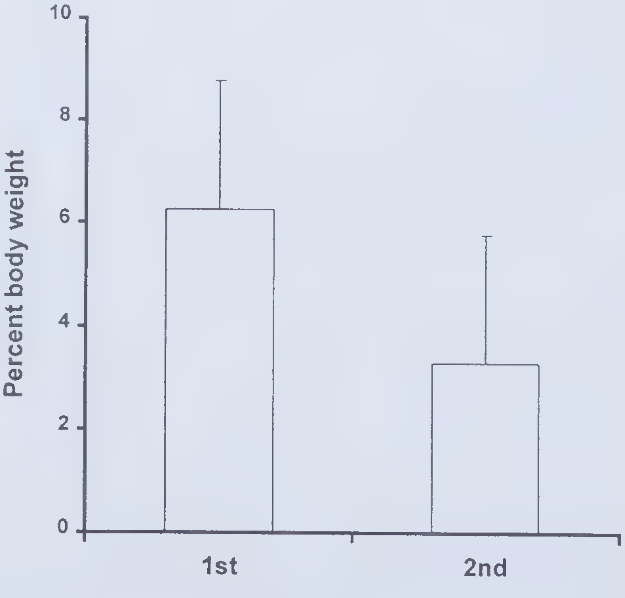

Figure 6. Mean spermatophore mass (± sd) as percent of body weight delivered to the female within 24 hrs after first and second matings (n= 6).

male prevents the female from feeding on the ejaculate. Indeed in some species of tettigoniids females are subject to a male-induced refractory period by the inclusion of chemicals in the spermatophylax (Gwynne 1990; Simmons & Gwynne 1991). The spermatophore is small in *P. ranatriformis* and the period of time between female mating attempts appears to be far shorter than that observed for other bushcrickets (e.g. *R. verticalis*, 3-4 days; Davies & Dadour 1989). We conclude that as females may remate within 1 day of the previous mating, the male does not deliver any material that will induce a postmating refractory period. Indeed, given the size of the spermatophore it may be advantageous to females to remate, so increasing the opportunity to sample more males and for males to control the size of the ejaculate (sperm number) if the female has recently mated.

That males attempt to interrupt other copulating pairs may provide evidence of positive selection on males to remain in copulation, at least until they have secured the spermatophore. If mate guarding occurs, even if only to prevent interruption and perhaps spermatophore displacement, then we may predict that copulation duration should increase in the presence of other males. Such a behaviour should be influenced by male density, however, we found no relationship in either of two series of trials which examined if male density influenced copulation duration between first and second mating.

For the first series, where males were allowed 2 females, copulation duration was 66.4 mins (± sd 63.1 mins; n = 19). However, copulation duration was longer, 101.7 mins (± 96.5 mins; n = 10), where males were exposed to females in the presence of other males. This difference between mean copulation duration, although in the expected direction, was not significant.

Agonistic behaviour. On no occasion did we observed male encounters in the field that could be classed as aggressive. However, although interactions were rare in the laboratory we twice observed males engaged in jousting by forcing the legs of the opponent from the substrate with the loser moving away from the winner. There were no females close by, and unlike male behaviour in the presence of a female, they did not curl their abdomen into a coupling position. Males were observed to compete for access to females by similar pushing behaviour with males trying to maintain contact with the female. On three occasions jousting over possession of the female resulted in the female moving away, and in one of these interactions the second male moved away once the first male had secured a grasp of the female. Males sometimes interrupted a second male's copulation by forcing the first male away from the female (n = 3). On 2 of these occasions the first male was successful, but in neither case did the intruding male attempt to copulate with the female. In two other instances the second male grasped the first male's abdomen, moving its claspers along the abdomen, but was unable to induce the first male to release the female. One male remained in this pseudocopulation position for 27 minutes. Although agonistic behaviour over territory may be weakly developed in this species, jousting behaviour should be considered part of the insect's normal behavioural repertoire.

Mating system

Mating in this species appears to be on or close to rendezvous plants where females remain feeding while males search between plants for both food and mates. There is no indication of any long range communication process, either by sound or chemical means. Substrate vibration, as incidental movement, could be expected to play a part in bringing the sexes together but there appears to be no rhythmic or patterned signalling. Where substrate vibration is important, morphological changes may be expected to enhance the detection of contact signals and the extreme body length, although undoubtedly having a cryptic function may, as in the phasmids, be advantageous in collecting vibratory information over a larger area of the plant.

Do males search for females? Our data on adult distribution indicate that males are more vagile than females, particularly as the season develops. That males were found close to a mating pairs suggests that males search for females, but the absence of any consistent male biased sex ratio in the "aggregations" indicates the need for more careful scrutiny of the encounter between the sexes in the field. It is possible that females remain at feeding sites and in the vicinity of competing males.

As with many polygamous species, where females remate within hours of the first copulation, the post-copulatory refractory period increases the likelihood that the first eggs laid by the female are fertilised by the most recently mated male's sperm (Thornhill & Alcock 1983). In bushcrickets the refractory period between repeated matings is dependent on the time of sperm ampulla attachment (Gwynne 1986; Weddel & Arak 1989; Simmons & Gwynne 1991) For example, in *Decticus verrucivorus* the refractory period is from 2 days when the ampulla is removed immediately after copulation, to 6 days when the ampulla remains attached for 3 hours (Weddel & Arak 1989). In *Requena verticalis* and *K. nartee* the spermatophylax is large, being > 20 % of the male body weight in the latter species (Gwynne, 1986; Gwynne & Bailey 1988) and in both these species nutrients from the associated spermatophylax contribute to the developing oocytes (Gwynne 1988; Simmons 1990). Spermatophore mass of *D. verrucivorus* constitutes less than 15 % of the males body weight with a mean of 9.45 % (Wedell & Arak 1989), and in this case it is just sufficiently large to prevent the female from consuming the sperm.

In *P. ranatriformis* the spermatophore is small, representing 10 % or less of the male's body weight and the spermatophylax is insignificant compared to the sperm ampulla. The spermatophore is not fed on by the female. As attachment time of the ampulla is critical for the release of any chemical that may induce a refractory period (see above) a female would have to remove the ampulla to decrease mating intervals. That female *P. ranatriformis* remate within 24 h suggests that no refractory period inducing -chemical is transferred in the ampulla. Further, that males can recognise prior mating during this period suggests that the spermatophore is acting as a sperm plug.

It is difficult to see any advantage for males to release a small ejaculate. Presumably, as there appears to be no mechanism of sperm displacement, or of sperm feeding by the female, the cavity under the subgenital plate would be filled. The most reasonable explanation for the small size of the second ejaculate in 3 of the 4 cases is that a male, once in copulation releases sufficient ejaculate to fill the sub-genital area. He stops because there is no more room.

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Position and developmental history of the central watershed of the Western Shield, Western Australia

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Abstract

Completion of the latest series of topographic maps at scales of 1:100 000 and 1:250 000 by the Commonwealth agency AUSLIG and of the 1:250 000 geological maps by the Geological Survey of WA has provided much new valuable data on the topography and surface features of the Western Shield in Western Australia. It has long been known that the Shield has a longitudinal central watershed or so-called continental divide separating drainages to east and west, and it is now possible to plot this precisely following contours on the new maps. The lateral watersheds bounding the catchments of rivers, still mainly active, which drain to the west coast have also been mapped. The central watershed rises steadily from 400 m asl at its southern end to a maximum of 750 m near its northern end, in conformity with a general tilt of the Shield. The lateral watersheds slope down gradually from the central watershed to ± 250-300 m at the western edge of the Shield, a height corresponding, it is suggested, to Cretaceous sea level. Metamorphic belts incorporated in the general granite-gneiss ground mass of the Yilgarn Craton have only very local effects on drainage patterns. On the Yilgarn Craton the mapped watersheds tend to be covered by sandplains, varying from complete cover in the south to partial in the north. Whereas the superficial deposits on these sandplains may be of different ages, i e subsequently disturbed, reworked or replaced, the saprolite beneath is suggested to conform to a palaeosurface resulting from planation during the Mesozoic era, when the drainage systems of today also originated.

Introduction

Geological terminology has been undergoing revision in recent years, and while the term Western Shield appears prominently in the Geological Survey's 1975 authoritative account of the geology of the State (Anon 1975), it does not appear at all in the 1990 edition (Anon 1990). None the less it is useful for geomorphological purposes as it defines a practical unit (Fig 1) of Precambrian rocks surrounded by Phanerozoic basins whose history and surface features are different. The Yilgarn Craton forms the southern portion with an area of 657 000 km^2 accounting for over half the Western Shield. It consists of Archaean granite and gneiss with infolded beds of meta-igneous and meta-sedimentary rocks known as "greenstone belts", and forms a plateau surface varying between 200 and 600 m above sea level, known as the Old Plateau (Jutson 1914), Darling Plateau (Cope 1975) or Yilgarn Plateau (Jennings & Mabbutt 1977; Mulcahy & Bettenay 1972). In the north is the Pilbara Craton, divided from the Yilgarn Craton by a complex belt of metamorphic sedimentary and igneous rocks known as the Capricorn Orogen (Anon 1990). Part of the smaller Albany-Fraser Orogen borders the Yilgarn Craton on the south.

A major feature of the Western Shield is a north-south watershed or divide (Fig 1) which separates the valley systems of rivers, some still active, draining to the west coast from those now largely inactive and disorganised which formerly drained east and south-east. This watershed runs north-south approximately central to the Western Shield equidistant from the margins of the sedimentary basins on either side (Fig 1). This watershed orientation could be expected for a tectonically inert continental peninsula twice as long as broad with sedimentary basins on each of the two longer sides (Beard 1973). This was the situation during the Mesozoic when the Shield was a peninsula of Antarctica, suggesting that its present drainage systems originated during that era (Beard 1973). The latter are unrelated to those which developed after uplift of the land in the Canning and Officer Basins in the Early Tertiary, which flowed north-west and south respectively from another principal watershed extending SW to NE between latitudes 22 ° and 25 ° (Beard 1973; van de Graaff *et al.* 1977).

Descriptions of the surface features of the Western Shield have declined in number in the past 20 years after active publication in the 1960s and 1970s, although new topographic and geological information has steadily continued to become available. New data are mainly derived from two sources. First, the latest series of topographic maps at scales of 1:100 000 and 1:250 000 (AUSLIG) have been recently been completed. These maps are contoured at 50 metre intervals and also show abundant spot heights, whereas few heights were previously available. They enable a much better appreciation of the conformation of river catchments and the major features of the Shield. Secondly, the 1:250 000 series of geological maps (Geological Survey of WA) conform to the grid boundaries and sheet names of the topographic series and provide a complementary treatment of surface features.

Jutson (1914) did not indicate the Central Watershed in his map of the drainage divisions of Western Australia

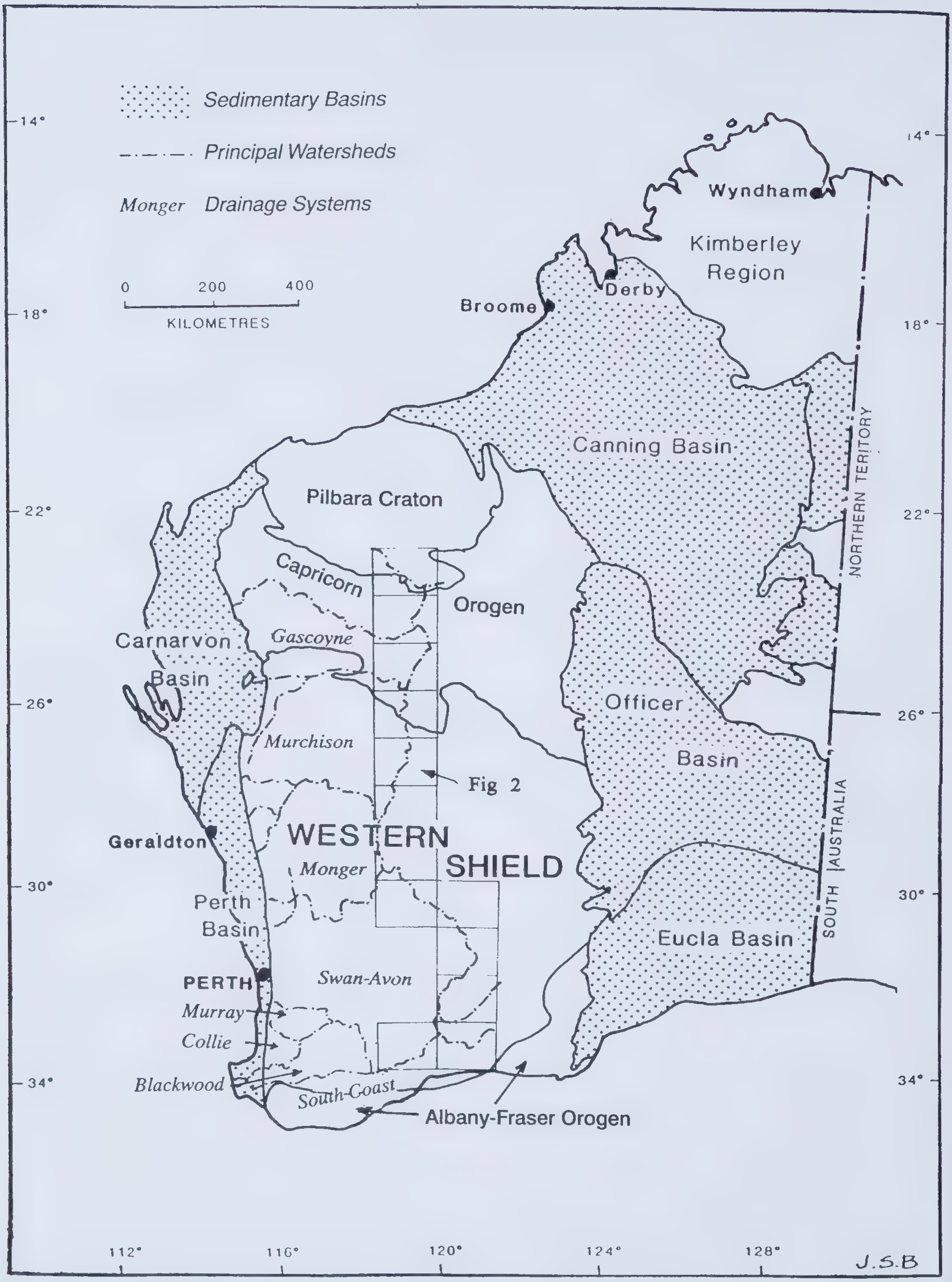


Figure 1. Simplified map of geological structure of Western Australia, based on Figs 3.1 and 4.1 in Anon (1990), to show the Western Shield, its subdivisions and surrounding sedimentary basins. Positions of the central and western lateral watersheds have been added, and drainage systems.

as it was not then recognised that the salt lakes of the interior (Jutson's "Salinaland") occupy the valleys of relict river systems. The southern part of the watershed was figured by Mulcahy & Bettenay (1972) as the "major continental divide", by Beard (1973) as the "principal watershed" and by van de Graaff *et al.* (1977) as the "major drainage divide" on their drainage system maps. The first of these terms has been used by Glassford (1987) and Glassford & Semeniuk (1995) as well as in a number of explanatory notes to geological sheets but seems open to objection as it is not strictly speaking a continental divide. I prefer "watershed" to "divide" and refer to the valley system of a particular river as a "catchment" to avoid confusion with the geological term "basin"

Methods

The surface of the Western Shield is mostly of low relief and so it has been difficult in the past to determine the alignments of watersheds and former drainage lines. This paper provides a precise plot for the position of the Central Watershed using modern topographic data to improve the sketch maps of previous authors. Data from vegetation and geological maps have been incorporated to show the conformation of the watershed and its surface features. The watershed was drawn following the contours shown on the latest series of 1:250 000 topographic maps. As it traverses relatively high ground, numerous spot heights, bench marks and trig points were available to establish precise elevations. On the granitic Yilgarn Craton, the watershed mostly traverses extensive sandplains where it was difficult to establish its exact position, so assistance was obtained from vegetation and geological maps. Within the Capricorn Orogen the watershed traverses mountainous country with ranges striking WNW-ESE to W-E which form transverse ridges across it with flat plains between them. In addition to the Central Watershed, the position and conformation of three main lateral watersheds were plotted and described in the same way, those dividing the Swan-Avon, Moore-Monger, Murchison and Gascoyne systems on the west side.

Results

The alignment of the central and lateral watersheds is shown in Fig 1 at small scale in relation to the Western Shield, and in Fig 2 at larger scale in more detail. All available heights on the alignments have been marked. For easy reference in Fig 2, the diagrams are divided into rectangles of latitude and longitude corresponding to the national 1:250 000 map grid, with the names of the map sheets indicated.

Central Watershed

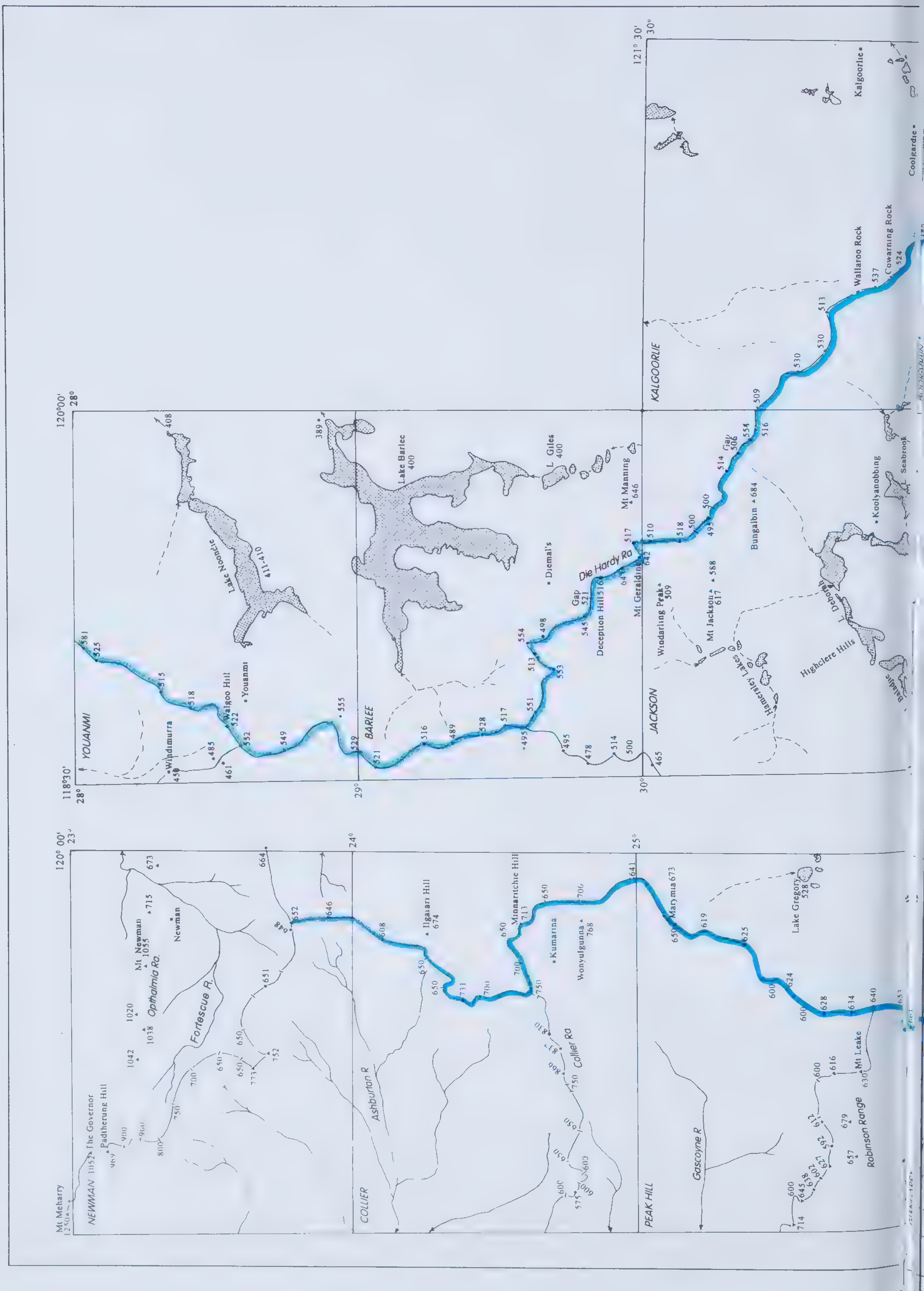
The Central Watershed extends from an undistinguished eminence 652 m above Australian Height Datum situated 45 km due south of the township of Newman in the Pilbara (map ref QU7769) to an equally undistinguished point at approx 400 m situated near Lilian Stokes Rock, 40 km due east of Lake King (map ref TD3040). It terminates at either end where it meets a transverse watershed delimiting drainage to the north and south coasts respectively. In the south this corresponds in part to the Jarrahwood Axis of Cope (1975). The Central Watershed extends from lat 23 ° 46 ′ S to 33 ° 3′ S, a linear distance of 1036 km but a much greater actual length of 1481 km, as the watershed twists and turns considerably.

The heights along the Central Watershed, while undulating, show a steady rise towards the north in conformity with the tilt of the Western Shield already noted by other authors (Lowry *et al.* 1972: Stewart *et al.* 1983). The lowest point on the watershed is at the southern termination; the highest is at the junction with the lateral watershed between the Ashburton and Gascoyne rivers at 750 m. The rise is therefore 350 m in 1000 km equivalent to a slope, slight but significant, of 1.2 ′. The highest point anywhere on the Western Shield is at Mt Meharry (1250 m) shown at top left on Fig 2, with a rise of 850 m in 1130 km, equivalent to 2.6 ′. This compares with the observations of the above authors, who calculated 1.5 ′ and 1.6 ′ for smaller portions of the Shield.

Locally, while on the Yilgarn Craton, the watershed is somewhat flat and traverses extensive sandplains, On the Lake Johnston, Boorabbin and Kalgoorlie map sheets in the south, the watershed lies entirely on sandplain for 326 km except for a single minor greenstone outcrop at Hatters Hill and occasional protruding granite rocks. Further north, more topographic diversity appears where greenstone belts cross the line of the watershed and where these contain resistant rocks such as banded ironstones, to form outstanding hills and ridges. Since the general strike of the greenstone belts is NNW-SSE, they tend to intersect the watershed at a low angle. They do not appear to have significantly influenced the location of the watershed and may appear elsewhere in isolated summits and ranges reaching greater heights but only locally affecting the drainage. Thus on the Jackson and Barlee maps a major greenstone belt intersects the watershed, and the summits of the Die Hardy Range coincide with the watershed from Mt Geraldine (642 m) to Deception Hill (516 m; Fig 2).

Other hills formed by greenstone outcrops in the vicinity *e.g.* Mt Manning (646 m) and Mt Jackson (617 m) are unconnected with it. Greenstone belts do not always have such marked topographic expression, and on the Youanmi map the watershed is intersected but shows no apparent change in its general heights. Further north, however, on the Sandstone map the Ballanhoe Peaks and the Montague Range both intersect the watershed whose course is unaffected in the first case but runs along the summit of the range for a short distance in the second. In between these hilly belts the watershed continues its even course, undulating very gently with a slight rise towards the north and situated for the most part on sandplains. On the Barlee and Youanmi maps, lateral watersheds diverge towards the west.

On the Glengarry map there is a low transverse "Unnamed Range" which marks the transition from the mainly granitic Yilgarn Craton to the Proterozoic metamorphics of the Capricorn Orogen. From here, northward, the watershed is underlain by rocks of varied lithology, some more resistant than others, which strike across it at a high angle, The watershed therefore crosses successive transverse ridges with plains between them.


NEWMAN
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BARLEE
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28°
29°
30°
120°00'
121° 30'
Mt Meharry
The Governor
Padtherung Hill
Opthalmia Ra.
Mt Newman 1055
Newman
Fortescue R.
Ashburton R
Ilgarari Hill 674
Minnarithie Hill 713
Kumarina
Wonyulgunna 768
Collier Ra
Marymia 673
Lake Gregory 528
Gascoyne R
Mt Leake
Robinson Range
Windimurra
Walgoo Hill
Youanmi
Lake Noondie
411-410
Lake Barlee 400
L Giles 400
Mt Manning 646
Diemal's
Die Hardy Ra
Deception Hill
Gap
Mt Geraldine
Windarling Peak 509
Mt Jackson 617
Hampton Lakes
Bungalbin 684
L Deborah
Highclere Hills
Baladjie
Kooltyanobbing
L Seabrook
Wallaroo Rock
Cowarning Rock
Coolgardie
Kalgoorlie

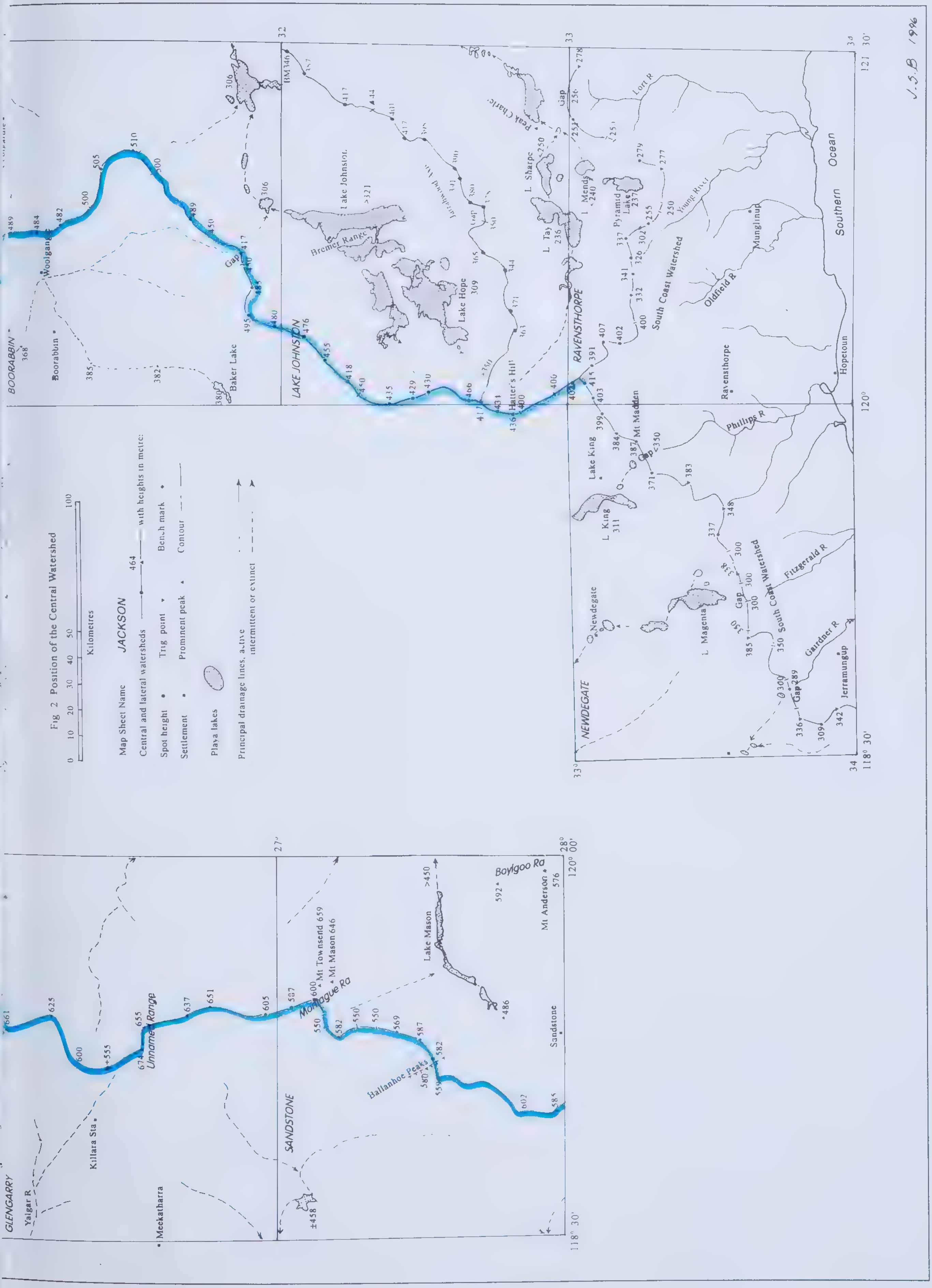

Figure 2. Detail of alignment of the watersheds.

This topography has evidently affected the location of the watershed to some extent since although it maintains its general northerly direction it is sinuous with a pronounced loop east of the Collier Range (Fig 2). The main watershed passes to the east of both the Robinson and Collier Ranges, both of which control lateral watersheds bounding the Gascoyne River catchment.

Height variations along the central watershed are remarkably small and there are no major gaps or irregularities. In a few cases there are minor gaps which may possibly indicate some change in the drainage pattern in the distant past. Beginning in the south, the first of these is a low point of 417 m on the Boorabbin map (ref TE7573). Over a length of 20 km the watershed declines in height from 495 m to this col, and rises again to 489 m in a similar distance. The col is a flat plain with scattered claypans and separates a north-trending palaeotributary of the Swan-Avon system from an east-trending chain of salt lakes leading into the Lefroy palaeodrainage (Clarke 1994). On the Jackson map there is a gap in the watershed with a minimum height of just under 500 m a little west of Mt Dimer (ref QM7838). This lies at the north- eastern end of a "major lineament" trending NE-SW which was identified in the geological survey (Chin & Smith 1983) as responsible for the south-west trending drainage line from the Clarkson Flats to Lakes Deborah and Baladjie, and attributed to crustal fracturing and Proterozoic dyke intrusion. A second similar gap occurs on the Barlee map just west of Deception Hill (ref QM2399). In both cases there is very little drop in level in these gaps where the col is at about 500 m but they do lie at the southern end of north-trending drainages of the Lake Barlee system. Further north there is only one conspicuous gap in the watershed, on the Glengarry map on Killara Station, where the watershed crosses a plain between two east-west ranges of hills at a col (ref QR208O) dividing east and west palaeodrainages. The col is 50-100 m below the general level of the watershed to north and south. Its significance may be no more than that it follows the trend of less resistant rocks within the Proterozoic sedimentary complex (Elias *et al*. 1982).

Lateral Watersheds

The alignments of the lateral watersheds bounding the Swan-Avon, Monger, Murchison and Gascoyne drainage systems to the west of the central watershed have been traced and mapped in the same way, and are shown at small scale in Fig 1. Presentation of the data in detail may more appropriately be reserved for later studies of the evolution of drainage in these individual systems which it is hoped to publish. Briefly, the Swan-Avon/Monger watershed leaves the central watershed on the Barlee map (Fig 2) at a height of 495 m at first in a south-westerly direction. With minor undulations it descends gradually from 495 m to 250 m at the Darling Fault, and has a total length of 410 km. It forms a continuous ridge without any noticeable low points or gaps, and is situated for its entire length on sand plains.

The Monger/Murchison watershed branches off on the Youanmi map at 552 m in height and is 455 km long to the edge of the Western Shield. This watershed is controlled by a greenstone belt for some 30 km from Mt Charles (639 m) to Dalgaranga Hill (642 m) where the country is hilly and reaches greater heights. Close to the eastern end the watershed has a pronounced gap which may have been associated with former drainage out of Lake Boodanoo. Otherwise the watershed maintains even heights of about 500 m along its eastern half and then descends gradually to 300 m at the edge of the Western Shield. Outside the greenstone belt patches of sandplain occur along its length.

The Murchison/Gascoyne watershed branches off from the central watershed on the Peak Hill map at an undistinguished point on a wide sandplain, altitude 640 m. For the first 100 km it is formed by ridges of the Robinson Ranges at heights of 600-650 m (max 714 m), but further west takes an even course descending to 300 m at the edge of the Western Shield. The total length is 400 km. There are no sandplains except at the start, but portions of the alignment have been mapped geologically (Elias & Williams 1980; Williams *et al*. 1983) as capped with duricrust, which I interpret as former sandplain from which the superficial sand has been removed. Fig 2 also maps part of the south coast watershed delimiting the numerous short streams flowing to the Southern Ocean, and the watershed dividing the Lefroy and Cowan drainages (Clarke 1994) which appears to represent the Jarrahwood Axis of Cope (1975).

Discussion

The descriptions of the central and lateral watersheds with their surface features may throw light on the nature and origin of the landscapes traversed, though landscape evolution on the Western Shield has been long and complex and many details remain unknown. Only the broadest framework of major episodes and phases can be presented here but may provide a first approximation for future testing and refinement.

The watersheds themselves and the drainage systems which they enclose are evidently of considerable antiquity, having been attributed to the Mesozoic by numerous authors *e.g.* Beard (1973), van de Graaff *et al.* (1977), Butt (1981) and Clarke (1994). On the Yilgarn craton the watersheds are mainly situated on sandplains - broad, sand-covered expanses of little topographic relief. Exceptions occur locally only where monadnocks of resistant rocks protrude or where the sandplain has been eroded away. The central watershed slopes up gently towards the north, suggesting a tilt of the Western Shield by epeirogenic movement. The lateral watersheds slope down equally gently from the central watershed to the edge of the Shield. The surfaces on which the watersheds are situated appear strongly to conform to a palaeosurface created by general levelling of the craton during Mesozoic time as suggested by Butt (1981) and completed by the mid-Cretaceous. The rise in sea level in the early Cretaceous would have prevented further down-cutting by the rivers, and the general levelling would have reduced erosion and silt-load. This is supported by the reduced thickness of Cretaceous sediments in the Perth Basin and the appearance of carbonates among them. The levelling would have provided a relatively inert surface beneath which deep weathering could take place as it has done generally on the Craton, and on which erosional material could accumulate without being transported outside the system. It is envisaged that by the mid-Cretaceous a gently undulating plateau had formed on the Yilgarn Craton, broken only by scattered monadnocks. It was covered largely by the products of its own erosion and drained by sluggish rivers in shallow valleys.

It is important to distinguish in this context between the surface as a landform and its superficial deposits. The landform is the surface of the superficial deposits which have accumulated on the saprolite to form a new land surface, the components of which are not necessarily directly related to the upper bounding surface of the buried saprolite. A relatively stable landform surface is clearly a necessity if deep weathering is to take place, in view of the time scale involved. Relative stability results when the products of weathering are removed from the surface at a slower rate than they are formed. Weathering can continue below the saprolite surface but once it is covered by superficial deposits there can be no more removal of weathered material from the saprolite other than by solution, and the buried surface remains stable without further lowering. It is therefore quite possible for surfaces of some antiquity to be preserved, as demonstrated by Nott (1995) in the Northern Territory. On the Yilgarn craton the Mesozoic palaeosurface is preserved beneath later sandsheets. It was formerly thought, following Prescott (1931) and Stephens (1946) that the profile under the sandplain represented a soil developed directly and *in situ* from the pallid zone but this view has been challenged. Glassford (1987) and Glassford & Semeniuk (1995) have shown that the upper portion of a typical profile (at least in areas studied) consists of a sandy clayrock overlying the weathered saprolite; this is turn unconformably overlain by sandy laterite, and capped by sheets and dunes of silicic sand. These deposits were named by the authors as separate geological formations and held to have been laid down as wash, dusts and aeolian sands, thereby burying a former landsurface. The age of these superficial deposits was held to be post-Eocene, in some cases as recent as Quaternary. While obviously reworking of the topmost Gibson Formation could be expected to occur intermittently down to any recent date, the sandy clayrock of the bottom-most Westonia Formation is more likely to have been laid down during the later stages of levelling of the Mesozoic surface. The difficulty is that the sandplains bearing these superficial deposits are not universal. They are limited to high ground capping watersheds, residual hills and mesas, and are not normally found in valleys where the soils are developed directly on saprolite. Such sandsheets as occur on lower ground are demonstrably of a different and later aeolian origin (Beard & Sprenger 1964; Beard 1981). The facts suggest that a universal palaeosurface once existed on which the superficial deposits were emplaced, and that this has later been dissected by valley deepening, and surface erosion.

If the general levelling and formation of the Mesozoic palaeosurface was completed by the mid-Cretaceous the superficial deposits must have been laid down already or soon after and subsequently dissected. Since the superficial deposits are considered by Glassford and Semeniuk (1995) to have been derived from wash, aeolian sands and dusts it is difficult to see how these could have been deposited on high ground only and not in the valleys, A post-Eocene date is too late for removal of valley deposits by fluvial action. By that time valley infill had become the dominant pattern. This difficulty does not arise if one adheres to the Prescott-Stephens view of the development of the sandplain profile since this would go on simultaneously with deep weathering and there is no need to postulate a post-Eocene date.

I suggest a more likely scenario as follows. High sea level prevailed in the early Cretaceous up to the Neocomian. After deposition of the Poison Hill Greensand in the Perth Basin the marine transgression began to recede, exposing a sedimentary surface (Playford *et al.* 1976). The Western Shield was effectively uplifted by an amount at least as great as the depth of the water offshore when the Poison Hill Greensand was being deposited. I am informed that as open marine conditions prevailed, a depth of 200 m should be allowed (A E Cockbain, pers comm). Since rainfall was high in the late Cretaceous and early Tertiary it is likely that the rivers lowered their beds to the new base level at the coast, and that the valleys were adjusted accordingly. A period of 30 million years from the Maastrichtian to the Upper Eocene is available for this process during which the sandplains could have been substantially removed and left capping higher ground as at present.

The landscape in the Capricorn Orogen is entirely different. For the most part it is controlled by a sub-parallel series of ridges of steeply dipping rocks forming north-facing cuestas, with country of more gentle relief between them. A Mesozoic surface may once have existed but it is difficult to find any trace of it now, due to active external drainage and erosion. In some valleys there are small duricrusted mesas formed from early, probably Tertiary, valley-fill. Sand sheets are found mainly along the central watershed and to its east on plains between the ridges and appear to be derived from decomposition of local quartzitic rocks.

Conclusions

1. This investigation more precisely locates the position of a central drainage watershed on the Western Shield.
2. On the granitic Yilgarn Craton the included greenstone belts have had no obvious effect on the general drainage pattern, which generally does not conform to the strike of these rocks. Ridges within greenstone belts may occasionally coincide with a watershed for a short distance but they have only local significance.
3. Within the Capricorn Orogen, where rocks are stratified and strike transversely to the central watershed, the general north-south trend of the watershed is maintained, but lateral watersheds are strongly influenced by the strike.
4. The central watershed rises steadily in altitude towards the north along its length which is consistent with the whole Western Shield having been subjected to a history of regional tilting.
5. Gaps or low points in the watershed, which may relate to prior drainage alignments, are few and appear to be of little significance.

6. The central watershed is of great antiquity and is likely to have been in existence since the Mesozoic. On the Yilgarn Craton it traverses a buried palaeosurface little modified since the Cretaceous. According to Glassford & Semeniuk (1995) this surface has been deep weathered and buried, thereby preserved, by lateritic dust and sandsheet deposits.
7. Lateral watersheds and any high ground within the catchments also tend to preserve portions of the palaeosurface and its superficial deposits, whereas in the valleys it has been eroded away by river action. It is suggested that this erosion took place between the Maastrichtian and the Upper Eocene.

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Microscopic analysis of 'engraved plaques' and other objects from Devil's Lair

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Abstract

Over twenty years ago some limestone 'plaques' and other unusual objects were excavated in Devil's Lair in the extreme south-west of Australia. Dated to the Late Pleistocene, they are almost unique in Australia. Their status has been questioned, and the present paper summarises the methods and results of a study of eight items from Devil's Lair, using methodology developed for examining rock markings. This involved, among other approaches, microscopic analysis, replicative procedures, geomorphological study and the systematic consideration of all possible alternatives in the context of the site's environment and human use. Some implications of the findings of this study are considered, especially within the context of 'taphonomic logic'.

Introduction

One of the most significant archaeological finds of Australia is the several marked limestone fragments from the Devil's Lair cave in the extreme south-west of the continent (Dortch 1976, 1984). Dated to the Late Pleistocene, three of these objects have been described as engraved plaques, in which respect they are almost unique in Australia. There is only one close parallel, a find from Koonalda Cave (Gallus 1971:115), while the only numerous portable engravings known from Australian prehistory are the 'cylcons' of western New South Wales (McCarthy 1967:75). The latter are undated surface finds, but the recent discovery of what appears to be a fragment of a 'cylcon' at the Late Pleistocene site at Cuddie Springs suggests that these mysterious objects may date back many millennia.

The status of the Devil's Lair plaques has been questioned (Bednarik 1991), and in resolving the topic of portable engravings from the Australian Pleistocene it is essential that the origin of their markings be established. The present paper describes the results of a detailed study of eight items of apparent portable art from Devil's Lair, using the methodology developed for the study of Palaeolithic engravings of Europe, portable stone objects of Eurasia and cave markings in southern Australia and elsewhere. In addition, the findings' broader implications for Australian archaeology are considered.

Devil's Lair is a small limestone cave near the south-western corner of Australia (Fig 1). Besides being one of the oldest radiocarbon-'dated' sites in Australia, the cave has yielded what have been described as several bone beads and pendants, a series of marked stone plaques and cobbles, limestone artefacts, and stone tools with hafting mastic adhering to them (Dortch & Merrilees 1973; Dortch 1979a, 1984). All of these finds are from Pleistocene layers, and they are rather exotic in the context of Australian Pleistocene archaeology. Many of the Devil's Lair finds are indeed unique, as similar material has not been found anywhere else in Australia. For that reason they have been subjected to ongoing debate, and recently the excavator, C E Dortch, has modified some of his identifications of the 1970s (Dortch & Dortch 1996) and had some of the controversial objects subjected to specialist study.

My analytical procedure for the Devil's Lair objects involved four separate phases. First I studied all relevant

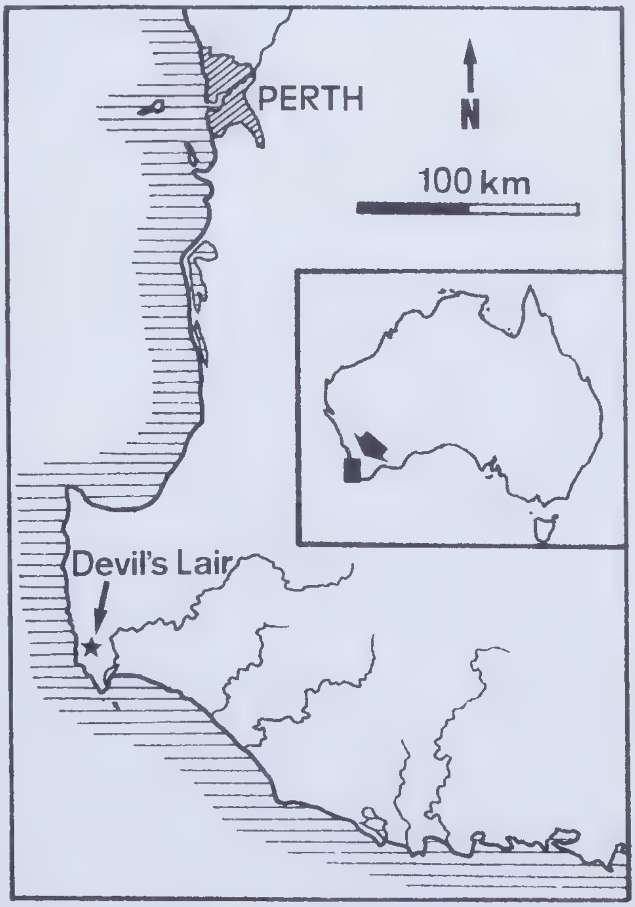

Figure 1. Location of Devil's Lair, south-western Australia.

published literature on the site, a total of about a dozen publications. This was followed by a thorough microscopic examination of each specimen, concentrating on the different types of surface markings. The marl pendant (Dortch 1980) was found to have certain diagnostic markings in its perforation and was studied separately (Bednarik 1997a). The third phase involved replicative experimentation with control material (limestone clasts from the site) and continual reference to the marked stones. During this phase I sought to develop a more detailed understanding of the mechanical properties of the aeolian limestone, a Pleistocene calcarenite consisting predominantly of calcium carbonate. It exhibits varying contents of quartz and other sand grains, whose size gradings and petrological make-up provide useful information. Finally, the fourth phase of the project involved more intensive microscopic examination of the marked 'plaques' on the basis of replication work, and by reference to previously examined similar types of finds. This final phase also involved various more specific approaches, such as the microscopic study of fractured quartz grains, determination of direction of movement in the production of markings, study of striation patterns, and systematic comparisons of animal claw mark sections on the same and other surfaces.

The Marl Pendant

On the basis of the excellent published descriptions I had expected that none of the specimens would bear

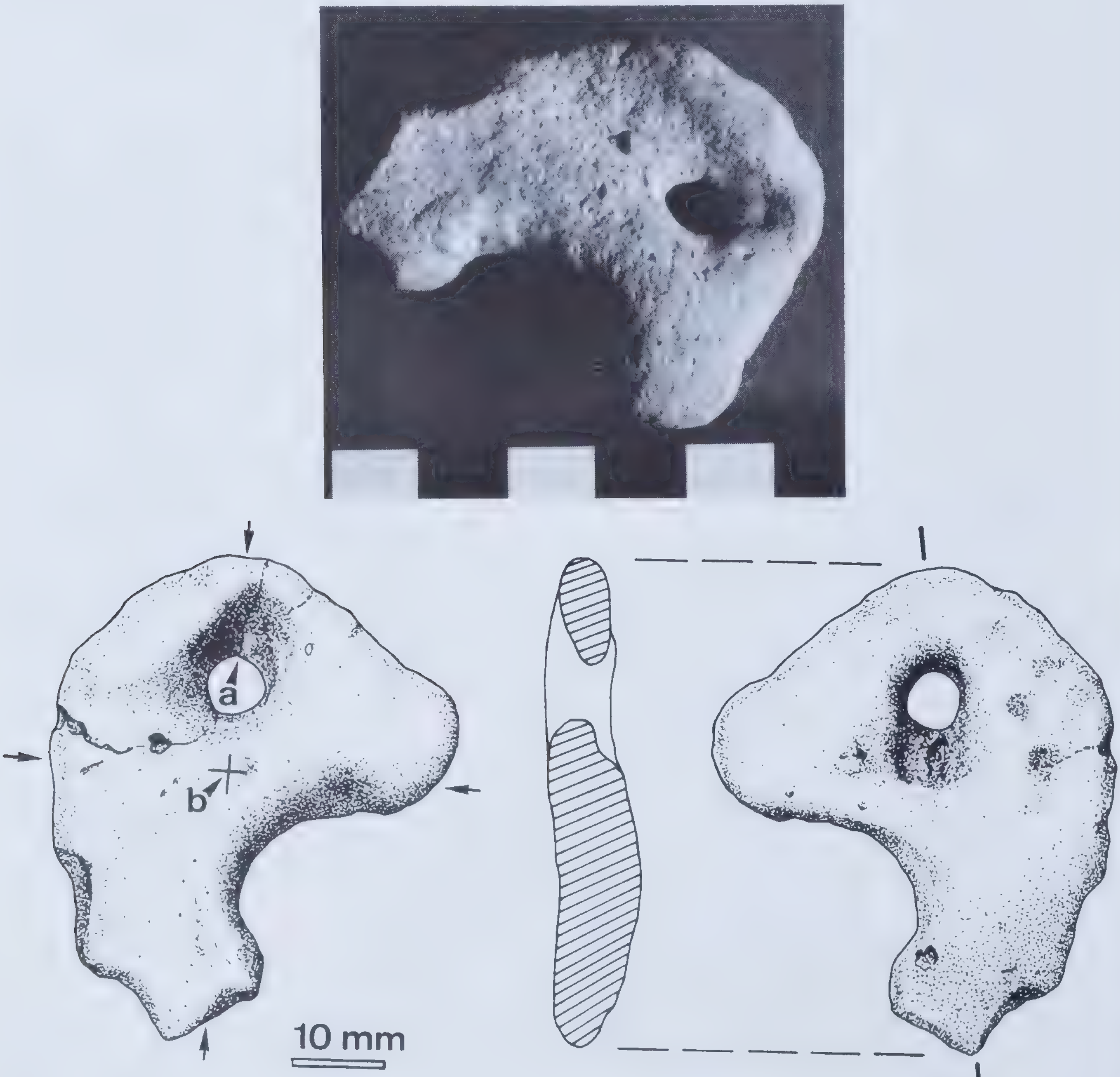

Figure 2. The Pleistocene marl pendant from Devil's Lair. The two sides and a section of the marl pendant, indicating the location of the wear grooves (**a**) and of the point of gravity (**b**). Adapted from Dortch (1980). Scale bars are 1 cm.

intentional markings, or provide any evidence of having been used as palaeoart objects, because the descriptions were consistent with taphonomic marks I had studied at hundreds of other sites. The perforated marl object had been described as having been drilled either by boring or gouging. The object bears a faint fracture line which follows an inherent structural weakness that has given rise to the formation of the perforation and other hollows, through natural weathering processes. The 6.5 mm diameter hole bears no trace whatsoever to indicate that it was drilled, enlarged, modified or reamed in any way by human hand. It is not circular or chamfered as drilled holes on experimental or Palaeolithic stone pendants generally are (Bednarik 1997b) and I conclude that it was formed entirely by natural attrition.

The perforated marl object weighs 18.65 g and measures maximal 55 mm (Fig. 2). It is from trench 8_7, layer 0, about 140 cm below datum, which stratigraphically indicates a Late Pleistocene age. The soft and porous 'marl' resembles the calcareous material that numerous Upper Palaeolithic stone objects of Europe were made from, such as the Willendorf No 1 figurine and many of the Russian figurines and fragments thereof (*e.g.* 24 figurines from the two Avdeevo sites and many more from Kostenki I; Bednarik 1990, 1995a). There are also numerous Palaeolithic marl pendants known from Russia, especially the 30 from Avdeevo Staraya, 145 from Avdeevo Novaya, and others from Kostenki, as well as many other objects of carved marl from these and other Russian sites. Thus the use of marl for the production of decorative or artistic objects is well known from the late Pleistocene.

The Devil's Lair marl object had been examined petrographically in the 1970s, which led to the conclusion that it differs from the coastal limestone the cave occurs in. Dortch (1980) therefore assumed that it must have been carried in from another locality.

In examining Pleistocene stone pendants for use traces of wear one focuses on the inside of their perforation. More specifically, the most important area is the perforation surface opposite the object's centre of gravity (*cf* Fig 2). This is where wear traces are usually present if a perforated object was used as a pendant. The inner surface of the perforation of the Devil's Lair marl piece bears four wear grooves (Fig 3). The first groove from the left is very shallow and wide, measuring up to 550 µm width. Next follows an almost V-shaped groove which still has a rounded bottom. It is 530 µm wide at its widest point, and as much as 240 µm deep. Quite close to this is the third groove, well rounded but shallow, and of up to 310 µm width. Immediately adjacent follows a wide, rather faint abrasion of maximal 750 µm width. One part of the deepest groove (the second) seems to provide a good indication of the size of the string that caused this marking. It includes a well-rounded section of 225 µm diameter, indicating the approximate diameter of the string.

These four abrasion or wear marks are distributed precisely across the surface where such wear would have had to occur if the object had been suspended on a string (Fig 4). The presence of several single marks alongside one another suggests that the object was not tied to the string by means of a knot, but was merely threaded onto the supporting cordage. There is no indication of the type

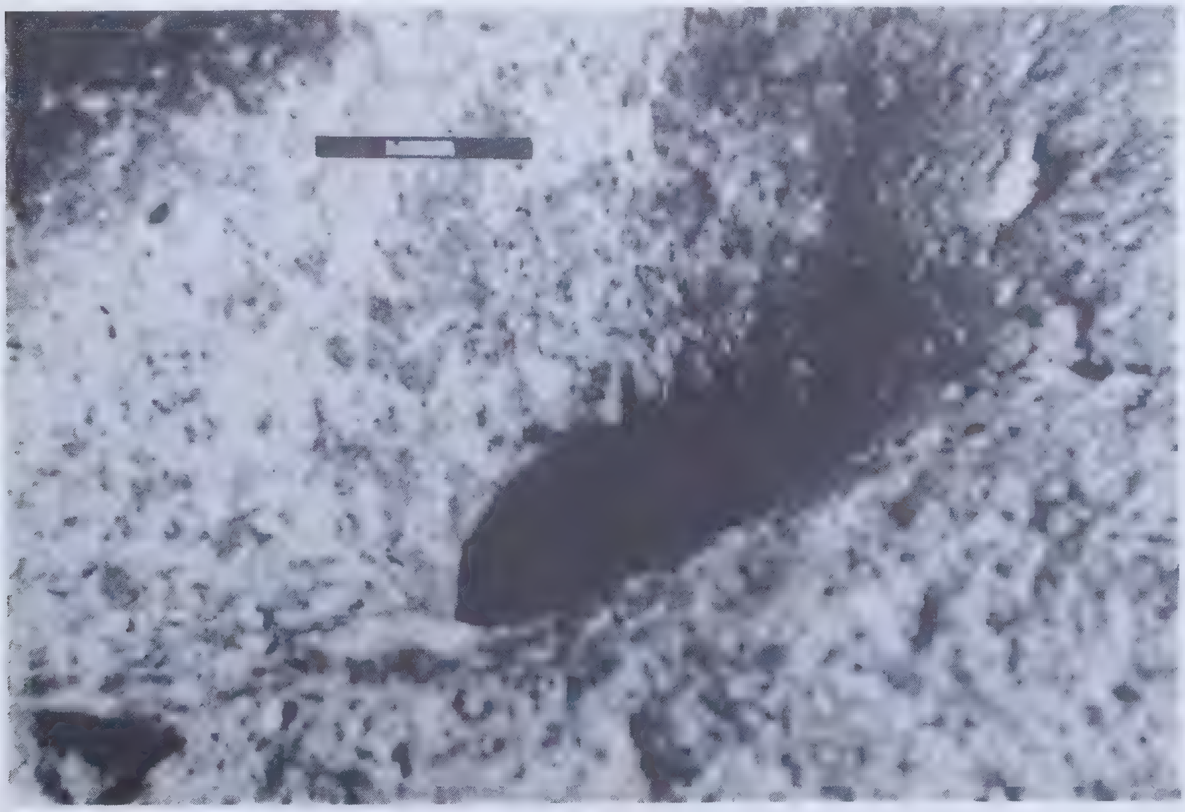

Figure 3. Microphotograph of the four wear grooves in the perforation of the marl pendant from Devil's Lair. Scale = 3 mm.

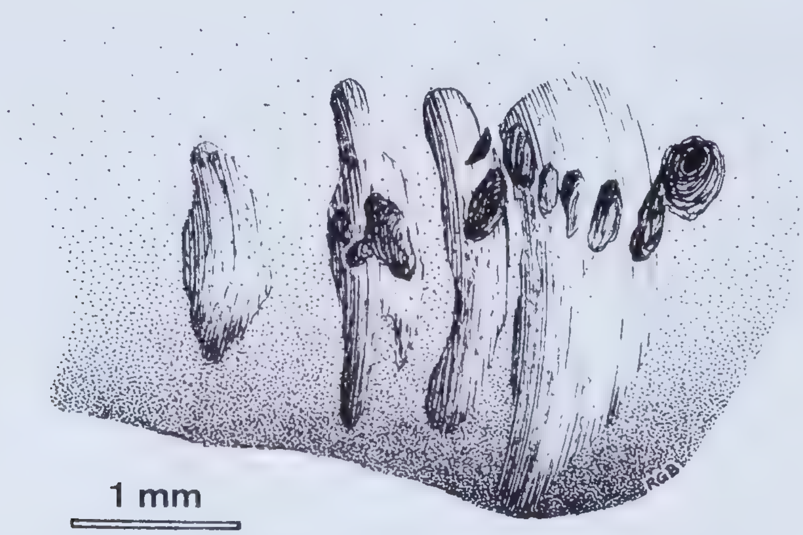

Figure 4. Detail of the four wear grooves on the marl pendant.

of string employed. In view of the extreme softness of the marl, the comparatively shallow wear grooves indicate that the object was not worn for a long time, presumably not more than a few days. There are no discernible markings suggesting that the pendant was worn suspended next to another perforated object.

Dortch (1980) considered and rejected the possibility that the object was utilitarian, *e.g.* used as a polishing tool for wooden artefacts or bone tools. I agree with his rejection of this possibility. The specimen's material is far too soft for this, and it entirely lacks wear traces that such use would have produced. Similarly, its use as a buckle or pulling handle (Boas 1888:Figs 15,17,121d; Nelson 1899:Pl 17; Kroeber 1900:Fig 8) can be safely excluded due to its fragility. It is of course possible that the piece was used as a weight for some purpose, but this does not seem likely in view of its very small weight. Among its possible uses, that of a pendant remains by far the most convincing, confirming Dortch's initial opinion.

This object is the only stone pendant so far recovered from the Australian Pleistocene. In Europe and Asia such stone pendants have been found at Palaeolithic occupation sites from France to Japan (Bednarik 1994a), and although a variety of materials have been used, marl is the most common for this application. It should be emphasised, however, that taphonomic logic (as defined in Bednarik 1994b) predicts a significant over-representation of ornaments made of stone, hence they are still to be regarded as rare, even in Europe.

Beads made of organic materials occur among archaeological finds in Australia, even of the Pleistocene and early Holocene. We already have several hundred such specimens (Morse 1993; Feary 1996) besides the three well-made bone beads from Devil's Lair (Dortch 1979b: Pl 2, 1984: 67). However, the stone pendant considered here remains the only early example of its kind in Australia.

Criteria for the Identification of Rock Markings

Among the basic classes of rock markings (see Bednarik 1994c for nomenclature), only a few are of interest in the present context; GK1 (general taphonomic marks), GK2 (clastic movement marks), BH2 (non-utilitarian anthropic marks) and especially BA1 (animal scratches). The latter are among the most common rock markings in the world, being about as common as glacial striae. Animal scratch marks have been thoroughly studied in over one thousand caves worldwide (Bednarik 1986a,b, 1991, 1992, 1993a, 1994c; *cf* Flood 1997:55) as well as at open sites. They occur in Australian caves and are particularly prominent in the continent's southern karst regions. Having never seen an Australian limestone cave that lacks animal scratches, I expect that all caves in the country contain this class of wall marking.

To recognise individual animal scratch marks requires considerable experience, because their morphologies differ greatly according to the species' climbing ability and method, 'speleo-behaviour', mobility, relative length of extremities, shape of claws or talons and their mechanics of application, and according to the shape of the claw points. The latter, for instance, can vary according to local conditions, the specimen's age, and so forth. Claw marks of Chiroptera (the most common of all animal scratch marks) may be quite different from those of similar-sized animals that are unable to fly (Bednarik 1991). Moreover, great variations can be caused by the lithology of the support rock (relative hardness, moisture content, relative air humidity, *etc*), and most particularly by modification processes (weathering, including speleo-weathering, the deposition of speleothems, and the deforming action of some precipitates, notably certain types of carbonate deposits). It is therefore necessary to appreciate that there are no simple, ready-made rules for discriminating between animal scratch marks and other, similar, rock marks. Rather this is a process of elimination in which many factors need to be taken into account, and in which alternatives have to be discounted systematically.

The empirical basis of this discrimination process consists of two bodies of evidence: the study of markings that can safely be attributed to animal species (*e.g.* megafaunal marks, which have been most thoroughly studied in Europe, such as those of *Ursus spelaeus*, and in

Australia; *cf* Bednarik 1993a), and the study of 'experimental' animal markings. The latter have involved a number of species, and in Australia especially possums. I have documented several instances of occupied possum dreys in limestone cavities (including in actual caves), and have microscopically surveyed the fresh climbing marks in the immediate vicinity of the occupied lairs of *Trichosurus vulpecula*. Marking experiments have also been conducted with live specimens, and their claws and claw spacings examined as part of this project. I have not conducted such experimental work with *Sarcophilus*, but have studied the very numerous claw markings in known lairs of the Tasmanian Devil, *e.g.* in Koonalda and Tantanoola Caves.

In Australia, four broad categories of animal scratch marks on rock surfaces have been distinguished (Bednarik 1991, 1994c). Large accumulations of claw marks are usually much easier to identify than isolated or single marks. One of the distinguishing characteristics refers to the relative positions of multiple marks constituting a 'set', and the relative course of individual grooves of a multi-pronged instrument such as an animal paw. Small rock fragments may only bear one or two grooves of a set (either exfoliated from a wall, or marked in situ within the sediment), which renders discrimination more difficult than on a cave wall. Nevertheless, other variables remain and can be consulted quite effectively in such cases, referring to the experience gained from parietal markings. These include;

1. Longitudinal striations are very frequently present in lines engraved with stone tools, and several distinctive forms are recognised by researchers as being characteristic. Animal scratches typically bear no striations.
2. Even if a claw did bear some irregularities which would produce striations, as may conceivably be the case, these would significantly differ from those occasioned by stone points. In the latter, the point is usually slightly turned over the course of a groove, which results in significant changes in the longitudinal striations. This is particularly clear at changes of direction. A claw point, forming part of a multi-pronged instrument, cannot be rotated in the same way.
3. Claw points are always rounded and comparatively symmetrical; stone points are rarely so.
4. In cross-section, a claw-caused groove is rather U-shaped, with the side walls steep, and *stries parasites* are never present.
5. Morphologically, claw marks are frequently of slightly 'cuneiform' appearance, *i.e.* with one end deeper and abrupt, and the other shallow and 'fading'. This applies especially to short marks.
6. Where such a mark is well preserved, the deeper and wider end can provide a fairly good impression of the shape of the claw point.

If the limestone is very soft, lines may have been incised by a material such as bone or even wood. This would be much harder to distinguish from claw markings than are stone marks, but there is no evidence of such tool materials having been used, in either Australian cave art or portable engravings on stone. I have conducted experimental work with dry and 'green' wood, bone, and other materials, including in south-western Western Australia (Bednarik 1988/89). Tool marks occur very frequently in about a dozen Australian caves we know of, and they have been studied in some detail in Nung-kol, Mooraa, Paroong, Ngrang, Orchestra Shell and Mandurah Caves. In all cases they could be demonstrated to have been made with stone tools, and the stone types of these tools were convincingly determined at two sites, from their distinctive striation patterns (Bednarik 1988/89, 1992). Much less work has been done on the systematic study of portable stone engravings in Australia (notably the hundreds of engraved cylcons) but preliminary work indicates that they were also fashioned entirely with stone tools.

Clastic movement marks are, as mentioned, also among the most common rock marks in the world, and they do occur in limestone caves. They have been described (Bednarik 1994c:33) as being attributable mainly to glacial action, fluviatile sedimentary movement, animal borrowing, gravity and tectonic movement (*e.g.* through adjustment in cave systems with a sub-floor phreatic reservoir). Such marks are most distinctive on cave walls rather than on clastic debris, and are easily recognised by their typical morphology where they are well preserved. Their size ranges from microscopic size to over one metre width. On sediment clasts they are likely to occur together with other marking types, such as animal scratches where they result from burrowing. They grade into 'general taphonomic marks', which include those caused by cryoturbation, solifluction and trampling. There are numerous examples on record, in most continents, where archaeologists described taphonomic, clastic and animal marks as anthropic engravings or rock art (many are listed in Bednarik 1994c).

Stone 'Plaques' from Devil's Lair

My interpretation of the six stone fragments with surface markings from Devil's Lair was not consistent with previous assumptions. Two have been described in

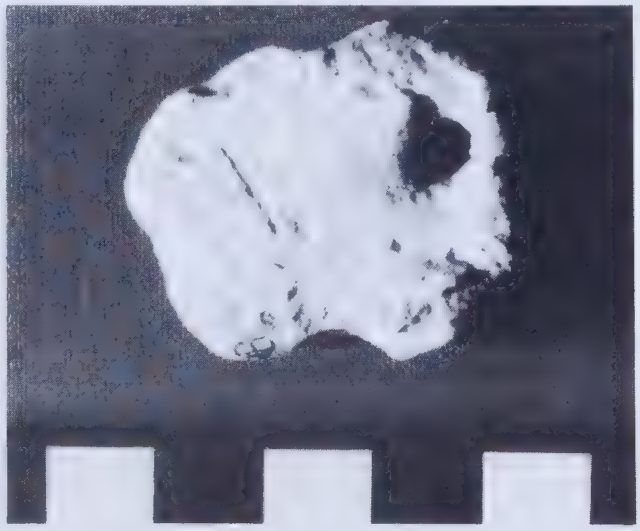

Figure 5. Naturally perforated marl fragment with single groove; No. B5348B. Scale bars are 1 cm.

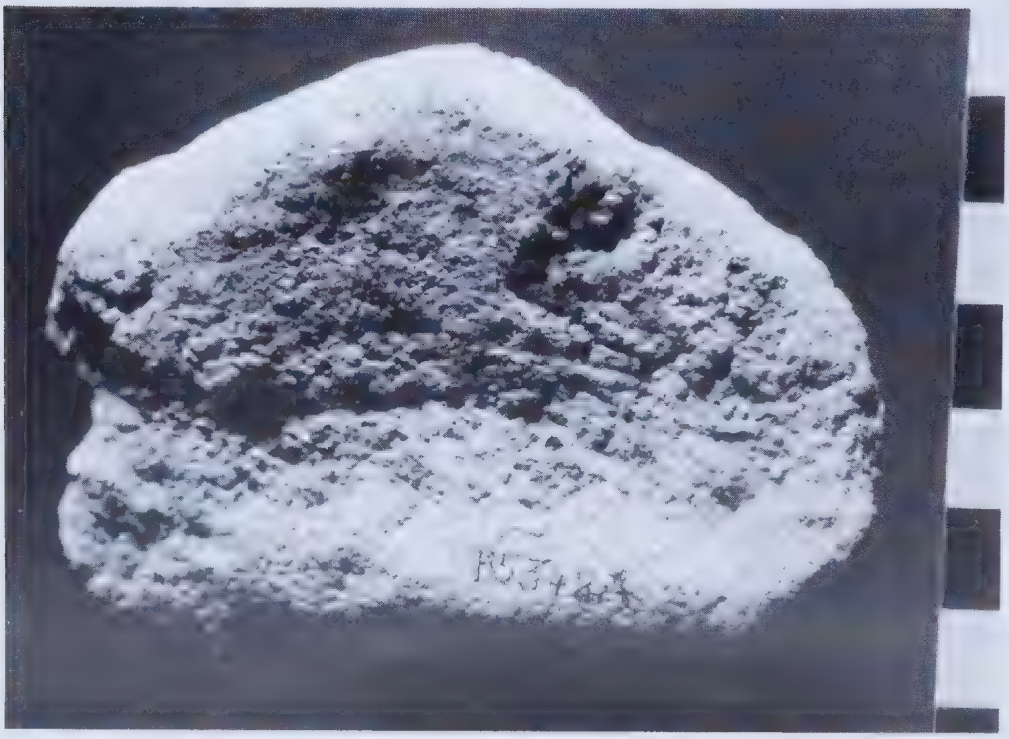

Figure 6. Limestone cobble bearing numerous animal scratch marks; No. B5348A. Scale bars are 1 cm.

detail and published as engraved plaques (Dortch 1976), and the others were considered as possibly having been engraved. All fragments consist of geologically recent aeolian limestone containing a small component of rounded quartz grains and in some instances other mineral grains.

B5348B (Fig 5) is from trench 10 south, layer 6, found at 210 cm depth. The small flattish stone fragment is especially soft, weighs 5.88 g and measures a maximal 36.6 mm. It bears a natural perforation which shows no wear marks. Numerous fine striations are apparently modern cleaning marks. The most distinct line marking

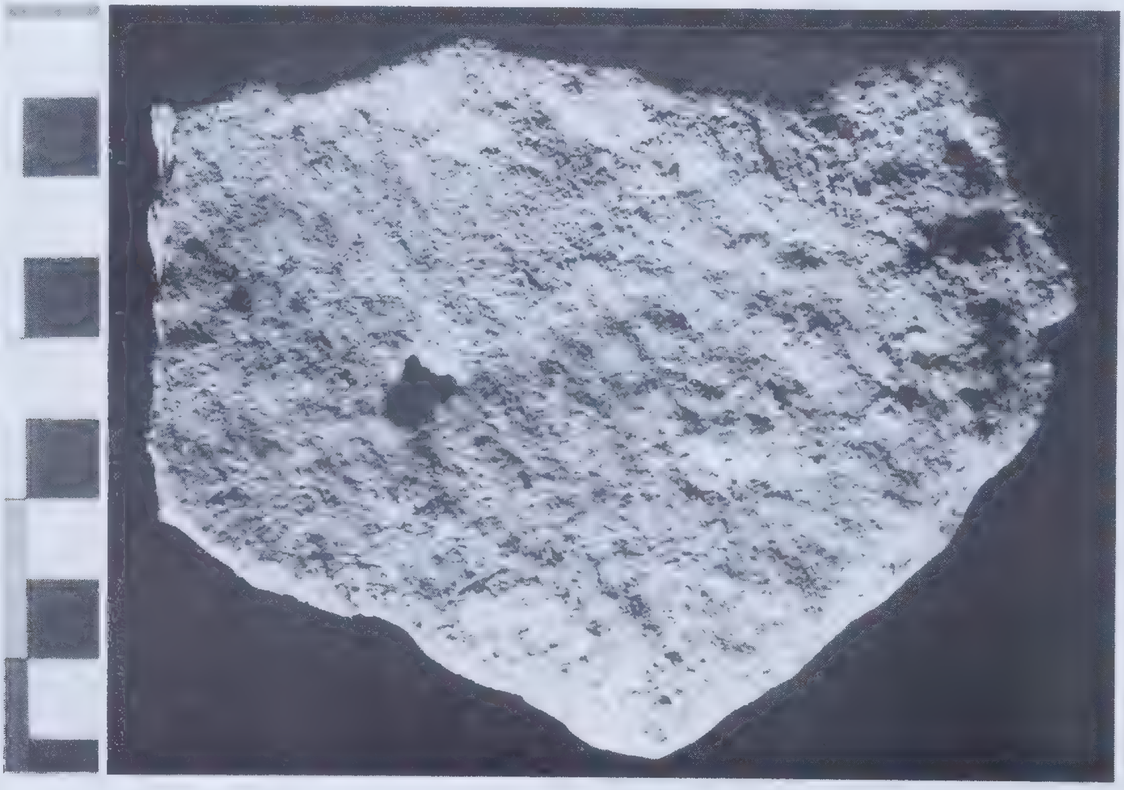

Figure 7. Limestone slab bearing remnants of fine taphonomic marks; No. B5300. Scale bars are 1 cm. Photograph by C E Dortch.

is 0.9-1.0 mm wide and has a well-rounded cross-section. This and the specific morphology of its starting point (cuneiform, indicating where the incising point first scored the very soft stone) suggest that this is an animal scratch mark (*cf* Bednarik 1991).

B5348A was recovered nearby and at the same depth. This 230.17 g limestone cobble has one flat and one convex side. It is 89.4 mm long. Linear markings are more prominent on the flat side and most are consistent with animal scratch marks (Fig 6). They fall readily into two quite distinctive groups. Of the larger group, a pair on the convex side has a 13.5 mm spacing. The smaller sets measure on average 415 µm between scratches (range 300-650 µm, n = 9). I interpret these small scratches as having been made by a small animal, up to mouse size. There is considerable evidence of the activity of such a species present on this surface, but it relates to moister conditions which would have rendered the stone significantly softer. Both the very small markings and the large scratches are not randomly orientated; they are predominantly in one direction and they occur as distinctive clusters. The marks in each cluster are similarly weathered, but clear differences in weathering are apparent between the clusters.

B5300, also from trench 10 but without secure provenance, is of plaque-like shape, weighs about 360 g and measures 122 mm (Fig 7). It has had a particularly complex history, including erosion by micro-pitting, exfoliation and deposition of calcite precipitate. Remnants of linear markings have survived the subsequent solution of much of the precipitate. One side has been rubbed against a similar flat surface under considerable pressure. Quartz grains that protrude from the surface have been pressure flaked and bruised, while similar grains embedded in the contact surface of another piece of stone have produced a variety of random linear markings on the formerly soft surface. The damage could have occurred through trampling or similar activity, or through sediment movement after the object became buried. The marking pattern suggests trampling as the most probable explanation, whether it was by humans or other animals. The second side of the specimen is almost unmarked.

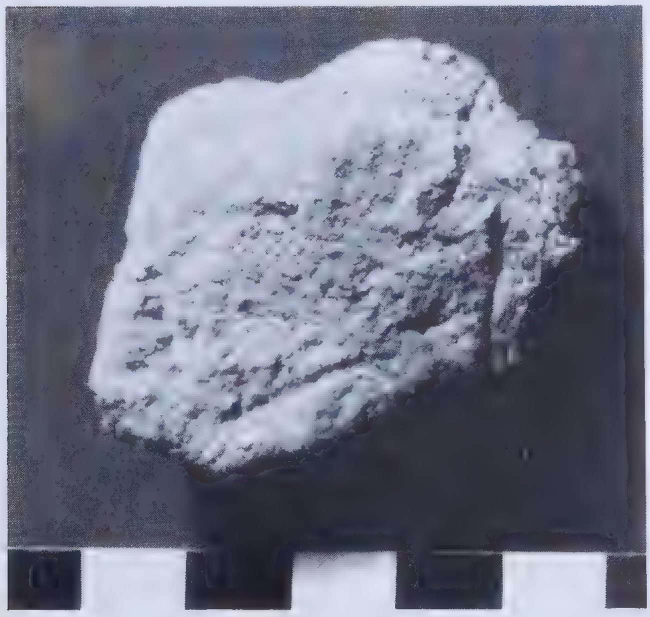

Figure 8. Limestone fragment bearing animal scratches; No. B3651. Scale bars are 1 cm.

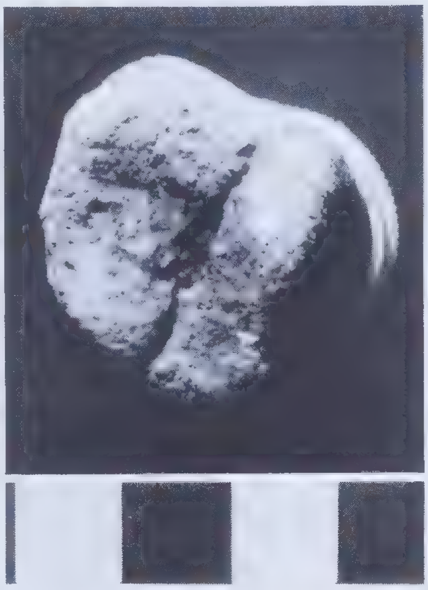

Figure 9. Small limestone fragment with deep marking; No. B3697. Scale bars are 1 cm.

Three pieces come from trench 9. B3651 weighs 18.66 g and is maximal 52.8 mm long. It has a higher content of quartz grains than the other specimens and is consequently harder (Fig 8). Nevertheless, it bears at least one mark that is 20 mm long, and a few shorter marks. The most numerous marks, however, occur near one end, where an accumulation of very short, 3-10 mm long scratch marks show spacings in the order of 1-1.5 mm between the points of the multi-pronged marking instrument. Some of the longer marks cross one of the larger and much older grooves.

B3697 is an irregular pebble of very soft, light-coloured 'marl'. It has one deep and prominent incision which curves around the surface profile (Fig 9). The groove is of well-rounded section, 1.5-2 mm wide, and is morphologically consistent with claw marks in hundreds of Australian caves. The pebble is 36.7 mm long and weighs 15.54 g.

The largest of the presumed plaques, B3652, comes from a depth of about 2.6 m. It measures 137 mm and weighs 180 g. This specimen has flaked off the cave wall or ceiling during the Late Pleistocene, judging by its stratigraphical position. The original outer surface bears several skins of re-precipitated calcite. The distinctive morphology of these carbonate speleothems indicates that the fragment is probably from a sloping ceiling area. There are almost no markings on this, the former outer surface, which demonstrates that the object was marked after it had become detached (*i.e.* on its 'inner' surface). Some recesses contain calcite-cemented sand grains, which shows that during burial, conditions were sufficiently moist to permit some further precipitation of calcite.

The linear markings are on the object's inside surface

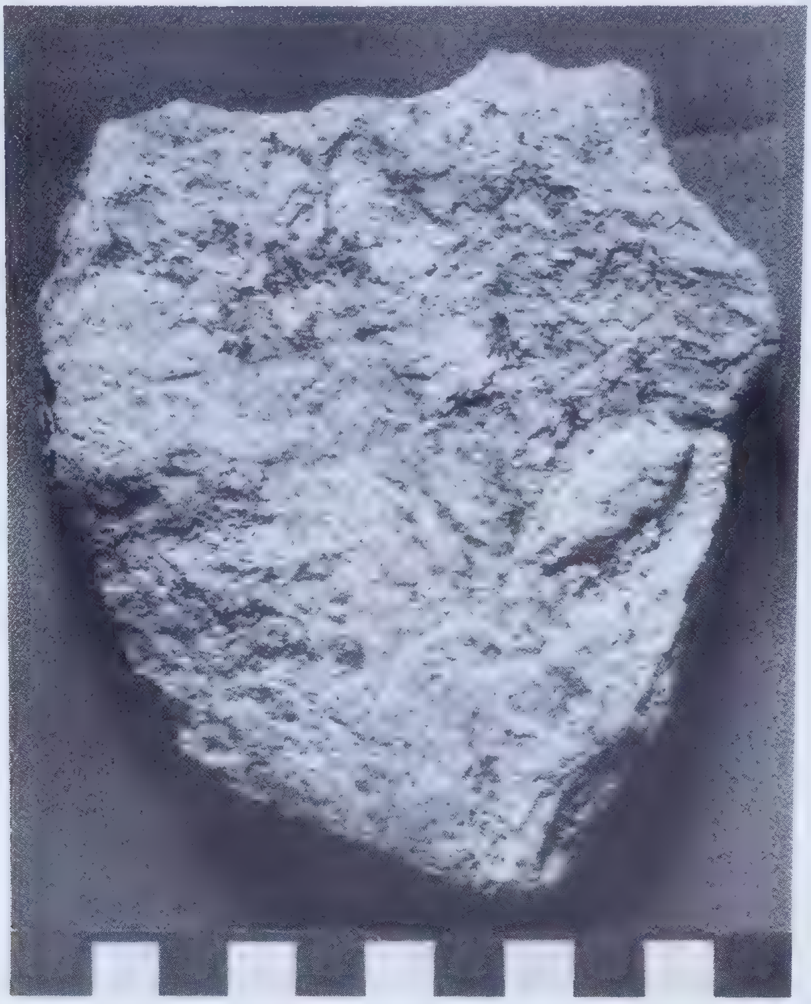

Figure 10. Plaque-like limestone slab bearing numerous taphonomic markings and some animal scratches; B3652. Scale bars are 1 cm. Photograph by C E Dortch.

(Fig 10). Among the most prominent are two sets of widely spaced marks which I interpret as animal claw marks, from their morphology, cross-section and course. The fact that they were executed in opposite directions suggests that these markings were made on an exfoliated fragment, and not on the rock face. These marks are spaced about 24 mm apart, which is well within the range of several possible species (*e.g.* Tasmanian Devil, large possums). Individual groove sizes and shapes are generally well rounded and range from 600-900 µm, but up to 1.1 mm in one case. These marks as well as most other marks on this specimen lack any striations or other indication that stone tools might have been involved. In the central part is a curved, meandering line with distinctive striations, 400-500 µm wide, with a pronounced depression at its point of commencement. This was probably caused by an irregularly shaped sand grain that was pressed hard onto the surface as it travelled over it erratically. Along its course it was forced over a red-coloured quartz grain embedded in the stone which it fractured and partly removed. Other markings on this surface include an accumulation of several slightly curved, very small marks near the upper left corner. Finally, the entire surface bears innumerable fine striations all over, especially within depressions. These were caused by nylon bristles, and many microscopic bristle fragments or shavings were found still attached to the surface. I have been informed that the specimen was cleaned with a soft toothbrush.

In summary, the six supposedly engraved limestone fragments from Devil's Lair bear a variety of taphonomic markings which present an initially confusing picture to the observer, but which can be untangled and analysed through detailed observation in combination with various replication experiments. There is not a single marking on these objects that I conclusively attribute to a stone tool, and there are very few that I consider might possibly be marks of stone tools from diagnostic characteristics such as longitudinal striations, *stries parasites*, and *sillons rectilignes* (*e.g.* d'Errico 1994; Bednarik 1992, 1994c, 1995b, 1977c). This is based on my experiments on rock samples from the site (the results confirmed entirely those of similar work at many other sites), and previous studies of animal scratches on rock involved a great deal of 'replicative' and observational work, relating to many mammalian and non-mammalian species. Among the many hundreds of macroscopic and microscopic markings on the Devil's Lair objects are kinetic markings caused by sand grains or projections from other stones, minute solution pits and animal scratches of various species, but numerically they are dominated by the traces of various types of modern damage.

Only one similar object has ever been reported from an Australian site, a small limestone fragment from Koonalda Cave with a few linear markings (Gallus 1971:115). I have proposed that it bears typical animal scratches (Bednarik 1991), which are extremely common on the walls and floor boulders of Koonalda Cave. Animal scratches, which are numerous in the caves of the Mount Gambier karst where they have been studied in detail (Bednarik 1991, 1994c), are comparatively less common in the far south-west of Australia, but I have observed them in all of the approximately twenty caves I have examined in that region (Bednarik 1988/89).

The Bone Sliver

The eighth object from Devil's Lair that I examined is a small bone sliver, 19.6 mm long, with a perforation near one end. It seems to be from the long bone of a bird. Dortch (1984:65) described it as a bodkin or pendant. In either case it should exhibit some wear on the rim of the perforation nearest to the broad end. I have searched in vain for such evidence, but the perforation itself was clearly made by human hand. It was first punched through from the convex surface, and the resulting hole was then lightly reamed with a stone point (Fig 11). Splinters of the punching action are still attached to the perforation, clearly indicating the direction of impact. The pointed end shows no use wear. I favour Dortch's interpretation that this was intended as a pendant, but perhaps it was used only briefly. Bone is much more resistant to wear than soft marl, and since the object weighs a mere 0.12 g it would not experience a great deal of wear from a supporting string. However, this is only speculation, and while the object is clearly an artefact I have not been able to determine its function reliably.

Discussion

While these objects from Devil's Lair are no doubt of Pleistocene age, I have avoided attaching specific ages to them and have not cited results of radiocarbon determinations. This is because the processing laboratory at Sydney University discovered a systematic error subsequent to its determinations relating to charcoal from Devil's Lair, when it was realised that the hand-made glass vials used on the old counter led to variations in the count rate (Temple & Barbetti 1981). Since only samples after December 1978 (beginning with SUA-963) were re-calibrated, the radiocarbon results from Devil's Lair (which are of earlier sample numbers) must be considered as imprecise, so I have not cited or discussed them here.

To summarise the current status of the Devil's Lair collection of objects, only material of doubtful status was submitted for examination by me. There is no reason to question the identification of the three bone beads from the site. Dortch's (1984:67) excellent photographs suffice to demonstrate their use as beads. There is solid evidence that the cave has yielded the only Pleistocene stone pendant so far discovered in Australia. A small perforated bone sliver is certainly an artefact, and may also have been a pendant. However, I interpret the markings on the various presumed stone plaques to not

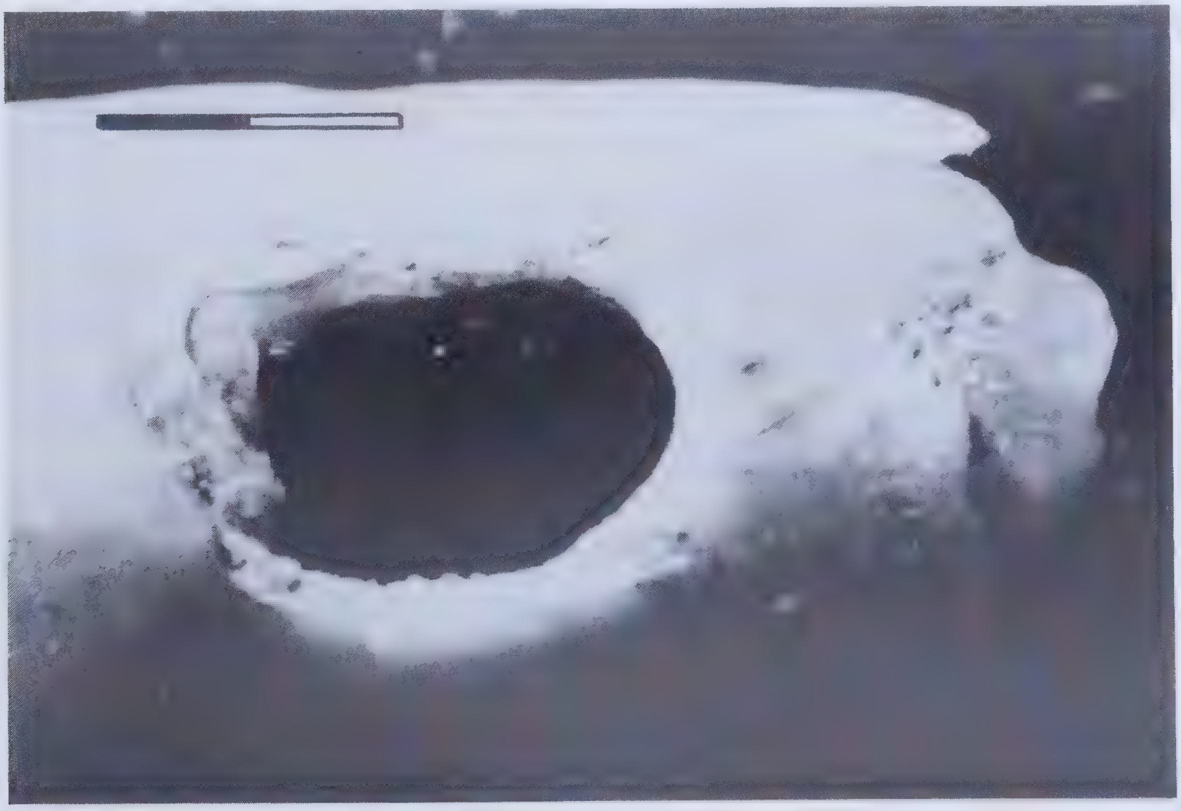

Figure 11. Microphotograph of the perforation in a small bone pendant; No. A22028. Scale = 2 mm.

be anthropic engravings. Rather, I attribute their markings to their often complex taphonomy and to recent damage.

Perhaps the most surprising aspect of this collection of five 'decorative' objects (presumed beads or pendants) from Devil's Lair is that they are not from a single layer, but are of widely differing ages. The three bone beads, for instance, are all from different sediment strata, and one is significantly younger than the two other. Why then do we have such a collection of unusual Pleistocene objects from a single site? The answer is probably taphonomic; these objects would have survived only in high-pH sediment conditions, *e.g.* in a limestone cave, and the number of suitable sites ever excavated in Australia is somewhat limited. Mandu Mandu Creek Shelter, where the only other Australian Pleistocene beads were found (made from marine shells; Morse 1993), is also a limestone site in a near-coastal region. This is hardly a coincidence, but is a fair reflection of preservation bias; such material survives only very rarely and in specific environments.

To appreciate the significance of this pattern of occurrence it is necessary to perceive it in its greater metamorphological context (metamorphology is the study of how forms of evidence change with time to become the forms as which they are perceived or understood by the individual archaeologist today; *cf* Bednarik 1995c). Beads or pendants had to be made in quite large numbers if such symbolic objects were to be imbued with social meanings, because it is repeated and 'structured' use which confers meaning on symbolic artefacts (Bednarik 1997b). Beads can be used in a number of ways or for several purposes, and provide various forms of information about the wearer and their status in society. They are not merely 'decorative'. Even if vanity were the motivation for wearing such items, stating this explains not why such items are perceived as 'decorative'. The concept is itself anthropocentric, we do not assume that other animals detect the information imparted by beads. In human culture, however, various forms of meanings may be encoded by such objects and in other kinds of body adornment. In ethnography, beads sewn onto apparel or worn on necklaces, for example, may signify complex social, economic, ethnic, ideological, religious or emblemic meanings, all of which are only fully understandable by a participant of the culture in question.

Beads and pendants cannot therefore exist in isolation, or have been used in small numbers only; it seems their use in any society could only be justified if they were used in large numbers. Wherever beads were used by recent people, they were typically encountered in large numbers, with individuals often wearing thousands (Anderson 1887:216; Dunn 1931). Yet, in the Pleistocene, beads occur very sparsely and in the earliest periods they are extremely rare. For example, only five bead specimens have so far been reported from the entire Lower Palaeolithic period (three in the Sahara, two in Europe; Bednarik 1997b). The entire Palaeolithic of India has yielded merely three beads (Bednarik 1993b). So, the Australian situation is consistent with that of the rest of the world. A notable exception is the three Streletsian burials at Sungir' in Russia, which yielded about 13 370 beads (Bader 1978).

The spatial and temporal patterns of occurrence of beads and pendants, especially in the Pleistocene, have to be explained through taphonomic logic and other metamorphological terms of reference, not in the traditional ways of archaeology. This shows that such patterns are found to be precisely as this form of logic (Bednarik 1994b:Fig 2) would predict them to be. Rather than interpreting these patterns as reflecting a paucity of such materials (Vishnyatsky 1994), they should be viewed as indicating a high probability that such artefact types were widely used.

Acknowledgements: I thank C E Dortch of the Western Australian Museum for initiating this study, for making the specimens available for analysis, and for providing two photographs. I thank also R Frank and D Frankel of La Trobe University for their support, and two anonymous referees for their valuable comments on an earlier draft. Any remaining shortcomings reflect my own limitations.

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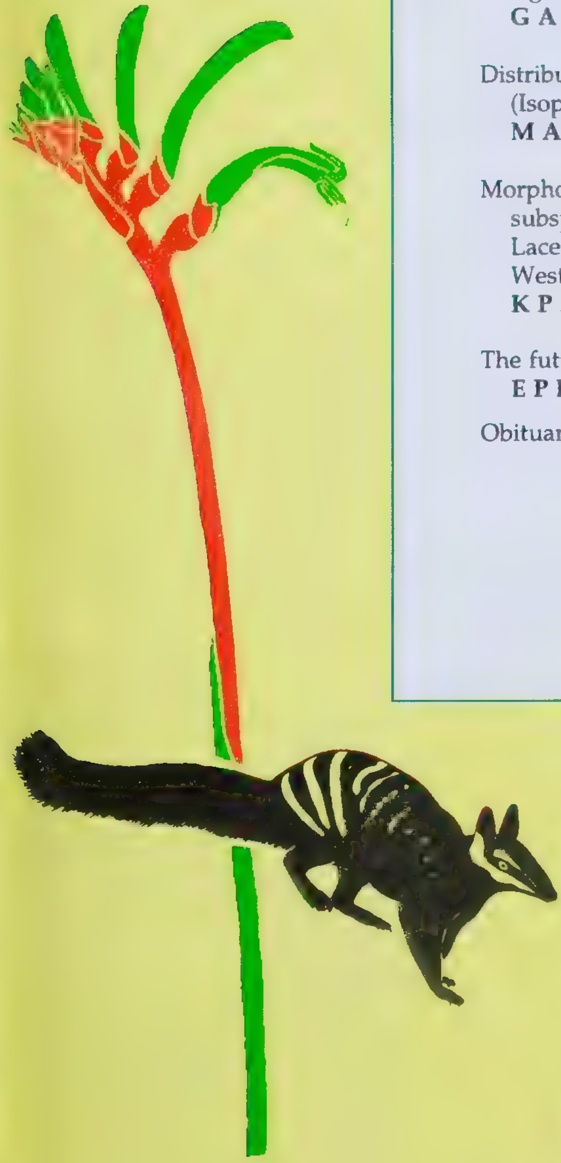

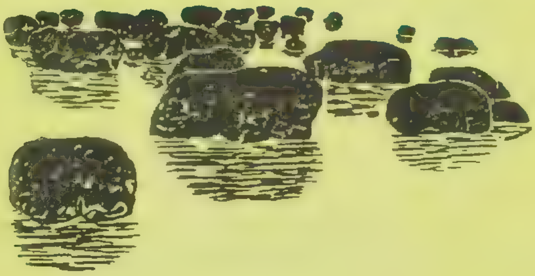

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Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences ambraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

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New species of *Calamoecia* and *Boeckella* (freshwater Copepoda: Calanoida) from Western Australia and Queensland

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Abstract

A small calanoid copepod, *Calamoecia halsei* sp nov, is described from shallow, turbid waters in claypans of the Carnarvon region of Western Australia. The genus *Calamoecia* Brady, which is endemic to the Australasian region, now contains 15 species. A larger calanoid copepod, *Boeckella timmsi* sp nov, is described from a shallow turbid claypan in Currawinya National Park located in Queensland just north of the border with New South Wales. The genus *Boeckella* de Guerne and Richard (which also occurs on sub-Antarctic islands, Antarctica and South America) now contains 21 Australasian species.

Introduction

Most calanoid copepods occurring in Australian inland waters are in the genera *Calamoecia* and *Boeckella*. As a generalization, the smaller calanoids (body length less than *ca* 1.4 mm, but *C. attenuata* is longer) belong to *Calamoecia* while the larger ones (female body length range *ca* 1.4 – 4.5 mm, but some including *B. minuta* are shorter) belong to *Boeckella*. Eight species belonging to those genera were described in the late nineteenth century and early twentieth century by the Norwegian carcinologist G O Sars, in some cases after rearing them in Oslo from resting eggs contained in parcels of dried mud consigned from Australia. The latter were part of an historic series of hatching experiments which resulted in the description of a significant portion of the freshwater lower crustacean fauna (Branchiopoda, Cladocera, Ostracoda and Copepoda) of Australia. *Boeckella minuta* was described in this manner in 1896 (Sars 1896).

Calamoecia was revised by Bayly (1961, 1962a) who recognised 12 species, to which were added *C. elongata* (Bayly 1979) and *C. zeidleri* (Bayly 1984). *Boeckella* was revised by Bayly (1964) with the recognition of 17 Australasian species, to which were added *B. bispinosa* (Bayly 1967), a New Zealand endemic *B. tanea* (Chapman 1973), and *B. shieli* (Bayly 1985). A comprehensive key to these two genera was published by Bayly (1992a). Now, after more than a decade without addition to either genus, a new species of both has come to hand at practically the same time in 1997 and the two are described below.

Methods

Specimens were measured under a Wild M7 stereomicroscope fitted with an eyepiece micrometer and dissected with tungsten needles in PVA-lactophenol mountant on a microslide under the same microscope. Appendages were examined (with bright field and phase-contrast illumination) and drawn using a Wild M20 microscope fitted with a Treffenberg drawing tube. The system of abbreviations given in full by Bayly (1992a,b) was used in the description of the first and fifth legs.

Taxonomy

Family Centropagidae Giesbrecht

Genus *Calamoecia* Brady

Calamoecia halsei sp nov

(Fig 1A–G)

Specimens examined

WESTERN AUSTRALIA (Carnarvon region): Chagra Well claypan, Jimba Jimba Station, 25° 11.78' S, 114° 57.04' E, 22.viii.1994, 10 female (mean length prosome 0.94 mm, mean length to end of caudal rami 1.35 mm), 10 male (mean lengths 0.73 mm, 1.04 mm); un-named claypan, Jimba Jimba Station, 25° 04.29' S, 115° 03.50' E, 22.viii.1994, 10 female (mean lengths 0.97 mm, 1.37 mm), 10 male (mean lengths 0.76 mm, 1.08 mm); un-named canegrass pan, Wooramel Station, 25° 40.87' S, 114° 13.23' E, 24.viii.1994, 2 female (mean length prosome 0.92 mm), 4 male (mean lengths 0.73 mm, 0.99 mm); un-named claypan, Coolcalalaya Station, 27° 31.49' S, 115° 05.24' E, 30.viii.1994, 7 female (mean length prosome 0.89 mm), 2 male (mean lengths 0.71 mm, 0.95 mm); ephermeral marsh, Brickhouse Station, 24° 57.85' S, 113° 42.27' E, 25.viii.1994, 1 male. All specimens collected by S A Halse.

Type material: Holotype male, allotype female, paratypes 30 male, 30 female. Holotype and allotype mounted on microslides, paratypes unmounted in vial. Western Australian Museum Crustacean Department registration numbers WAM 639–97 to 641–97. Type locality: Chagra Well claypan, 25° 11.78' S, 114° 57.04' E.

Description of male

Size: Length of prosome 0.68 – 0.81 mm, length to end of caudal rami 0.90 – 1.13 mm.

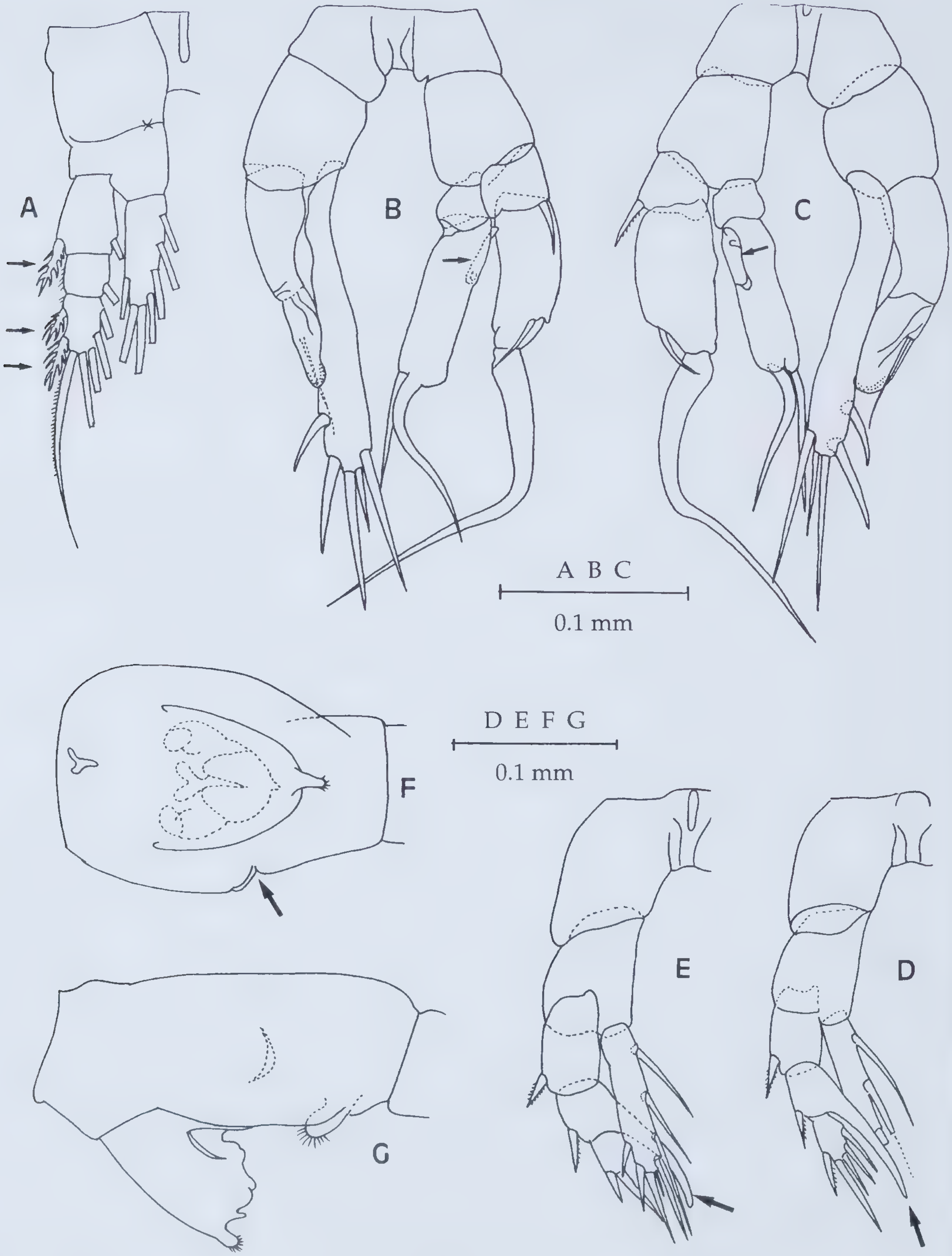

Figure 1. *Calamoecia halsei* sp nov; **A**, leg of first pair (drawn from male but identical in female except for larger size) [see text regarding arrows]; **B** & **C**, posterior and anterior aspects, respectively, of male fifth legs [arrows point to a unique, diagnostic feature]; **D**, leg of female fifth pair, showing whole of exopodite; **E**, as for D but showing whole of endopodite [arrows in D and E point to unusually long process from middle exopodite segments]; **F**, ventral aspect of female genital segment [arrow points to distinctive ridge and furrow on right side]; **G**, left lateral aspect of female genital segment (position of ridge and furrow located mid-laterally on right side shown by dotted crescent).

First legs (Fig 1A): Outer edge spines on Re1 and Re3 (see arrows Fig 1A) unusual within freshwater Centropagidae in having abnormally large secondary spinules. [These elaborate outer spines not occurring on exopods of legs 2–4].

Fifth legs (Fig 1B,C): Right Re claw bent through almost a right angle, lacking an inner spine. Right Ri 2-segmented with Ri2 four times as long as Ri1; Ri2 with upraised subrectangular thickening near proximal outer corner on anterior face (unique feature – see arrow Fig 1B,C) and typically with two spines at extremity – a large outer curved hook or claw and a smaller inner straight or slightly curved spine [extremity sometimes (observed one specimen in 15 examined) with third small, straight inner spine]. Left Re 2-segmented; Re2 spatulate or spoon-shaped (often bent out of alignment shown in Fig 1B,C because of fragile nature) with smoothly rounded extremity marked with minute pits or dots, and with seta inserted little short of half-way along outer edge. Left Ri 1-segmented, very elongated and exceeding left Re in length, typically armed with five spines of which four are terminal (second from inside shortest with remainder sub-equal) and one sub-terminal on outer edge [sixth spine sometimes (observed one specimen in 15 examined) present on inner edge, short distance from extremity].

Description of female

Size: Length of prosome 0.81 – 1.00 mm, length to end of caudal rami 1.13 – 1.45 mm.

First legs: Outer edge spines on Re1 and Re3 as described for male.

Fifth legs (Fig 1D,E): Outgrowth from inner distal corner of Re2 (the structural feature that is of key importance in defining the family Centropagidae) long, slender and only slightly curved, *extending almost to extremity of long terminal spine on Re3 (and sometimes beyond).* In several species of *Calamoecia* this outgrowth does not reach past the end of Re3 excluding its terminal spine; *cf C. gibbosa* where this structure is relatively massive and strongly curved (Bayly 1979, Fig 3E,F). Re3 typically with 5 spines (3 subequal on inner edge, 1 long terminal and 1 short on outer edge) but sometimes (1 in 12 legs examined) with only 4 spines (2 only subequal ones on inner edge). Ri 1-segmented, with a total of 7 setae (4 on inner edge, 1 terminal and 2 on outer edge) plus relatively short, thin spine immediately to inside of terminal seta.

Urosome: Genital segment (Fig 1F,G) about 1.3 times as long as maximum width viewed ventrally or dorsally, with thickened ridge and indentation mid-laterally on right side about one third length of segment from posterior edge (see arrow, Fig 1F).

Remarks: If one attempts to key out this species using the dichotomous key given by Bayly (1992a) the following key numbers would apply; 1, 2, 3, 5 and 7. Dichotomy number seven accommodates *C. australica* Sars 1908 and *C. canberra* Bayly 1962, both of which are distinctly different from *C. halsei*. In terms of secondary sexual structures *C. halsei* is most closely related to *C. zeidleri*, *C. australica* and *C. canberra*. This group of four species share the following features in the male fifth legs;

a) the right Re claw is without an inner spine

b) the right Ri is 2-segmented with Ri2 exceeding Ri1 in length by at least three times

c) the left Ri is 1-segmented, very elongated, considerably exceeds the left Re in length, and bears five spines of which four are terminal and one sub-terminal on the outside.

Although I have drawn attention to the unusually elaborate spines on the outer edge of the exopods of the first pair of legs (Fig 1A) of *C. halsei*, it should be noted that these appendages have not been described for all species of *Calamoecia*. However, it can be said confidently that they do not occur in all species; they are absent, for example, in *C. lucasi*, the type species of the genus (New Zealand material of this species examined for this feature by the author in July 1997), *C. australica* (Sars 1908, Plate ii, Fig 13) and *C. tasmanica* [see drawing by Sars (1912, Plate vii, Fig 9) of *Brunella longicornis*, which is a junior synonym of *C. tasmanica*]. The latter drawing of Sars also shows no outer spine on Re1 (formula for outer exopod spines 0.0.2) whereas this spine is present in most species of *Calamoecia* (corresponding formula 1.0.2; Fig 1A).

Most of the material examined here came from very shallow, highly turbid (turbidity 10,000–36,000 NTU) pans that contained decidedly fresh water (TDS 190–550 mg L^{-1}, K_{25} 140–920 µS cm^{-1}). The ephemeral marsh was a little less turbid (9,100 NTU) and slightly higher in electrolytes (K_{25}1,110 µS cm^{-1}) but still fresh. (Chemical data from S A Halse, CALM, unpublished observations.)

Derivation of specific name: Named for Western Australian limnologist S A Halse, who collected all the material of this new species and drew it to my attention.

Family Centropagidae Giesbrecht

Genus *Calamoecia* Brady

Calamoecia cf lucasi Brady

(Gascoyne-Murchison form)

Calamoecia lucasi Brady. The Cue population, Bayly, 1984, pp 149–150, Figs 4A–D.

Specimens examined

WESTERN AUSTRALIA (Carnavon region): Dywers Pan, 24° 26′ 00″ S, 114° 27′ 18″ E, 19.viii.1994, 10 females and 10 males, collected S A Halse.

Preliminary reassessment of taxonomic status

Bayly (1984) referred a form of *Calamoecia* collected from a pond near Cue to *C. lucasi*, In doing so, I pointed out that the Cue form differed significantly from populations in eastern Australia and New Zealand in several features involving secondary sexual structures. I now find that the above Carnarvon material, which agrees exactly with the Cue population in the male and female fifth legs and the female genital segment, can be clearly distinguished from *C. lucasi* sensu stricto, by structural features that are not of a secondary sexual nature. On the terminal exopodite segments of the first pair of legs of the Western Australian forms, the two outer edge spines each have three or four large secondary spinules along both edges, and the outer edge of the stoutest terminal spine has more than 25 large secondary spinules. In brief, these three spines are closely similar to, if not identical with, those in *C. halsei* sp nov (*cf* Fig 1A). In *C. lucasi* sensu stricto, however, these three spines have more numerous and extremely fine hair-like outgrowths along their edges. I now think it very probable that the "Gascoyne-Murchison form of *C. lucasi*" is, in fact, a new species, but I do not wish to proceed with a formal description at this stage.

Family Centropagidae Giesbrecht

Genus *Boeckella* De Guerne & Richard

Boeckella timmsi sp nov

(Fig 2A–E)

Specimens examined

QUEENSLAND: Claypan, near Coomburra Waterhole, Currawinya National Park, 28° 47' S, 144° 22' E 24.vii.1996; 7 females (mean length prosome [measured mid-dorsally to exclude large "wings" on last prosomal segment] 1.45 mm, mean length to end of caudal rami 1.98 mm), 10 males (mean length prosome [measured mid-laterally] 1.14 mm, mean length to end of caudal rami 1.51 mm). Collected by B V Timms.

Type material: Holotype male, allotype female, paratypes 13 male, 12 female. Holotype and allotype mounted on microslides, paratypes unmounted in vial. Queensland Museum registered numbers QMW22252–4.

Type locality: Claypan 1.5 km north-east of Coomburra Waterhole, Currawinya National Park, 28° 47' S, 144° 22' E.

Description of male

Size: Length of prosome measured mid-laterally 1.00–1.16 mm, length to end of caudal rami 1.45–1.62 mm.

Fifth legs (Fig 2A,B): Right Ri sub-triangular, attached more proximally on inner edge of right B2 than is typically the case, 2-segmented (Fig 2A) or 3-segmented (Fig 2B) with the second, or more distal, line of segmentation being often weak or absent, proximal inner projection commonly somewhat differentiated from remainder of Ri (Fig 2A), distal extremity sharply pointed (Fig 2B) or bluntly rounded (Fig 2A) reaching just less than half-way along inner edge of right Re2. Left B2 with projection at inner distal corner reaching to end of left Ri1 and armed with 10–20 very fine teeth. Left Ri 2-segmented with terminal segment (Ri2) sub-circular and extending about 0.6 times distance along inner edge of left Re1. Left Re1 short relative to right Re, distal extremity lying directly opposite a point only 0.4–0.5 times distance along inner edge of right Re2. Left Re2 (proximal portion of left Re claw) with prominent outer spine inserted at 0.25 times distance along segment and commonly (about one-third of population; Fig. 2B) with second (much smaller) outer spine inserted at 0.75 times distance along segment (this second outer spine on the left Re2 is not a normal feature of any other Australian species of *Boeckella*, but does occur as an invariable feature in some South American *Boeckella* such as *B. calcaris* and *B. palustris*).

Description of female

Size: Length of prosome measured mid-dorsally 1.42 – 1.49 mm, length to end of caudal rami 1.91 – 2.03 mm.

General body proportions (Fig 2D): More robust than most limnetic congeners; prosome 2.2 times as long mid-dorsally as maximum width (viewed dorsally or ventrally), and 2.35 times as long as urosome excluding caudal setae. Antennules relatively short, not reaching beyond end of prosomal "wings" when extended posteriorly. Last prosomal segment produced posteriorly on both sides into large "wings" or lobes reaching to posterior margin of urosome segment 2.

Fifth legs (Fig 2C): Re3 with 7 spines – 4 on inner edge, 1 terminal (exceeding Re3 in length) and 2 on outer edge. Ri 3-segmented, reaching to end of Re2 excluding inner process, setal formula 1.1.222.

Urosome: Genital segment (Fig 2E) with highly distinctive shape, squarish, length not greater than maximum width viewed ventrally or dorsally, with two rounded outgrowths and concavity between them on both sides.

Remarks: If one attempts to key out this species using the dichotomous key provided by Bayly (1992a) the following key numbers would apply; 1, 2, 5, 6, 7, 8 and 9. This is a pathway that leads to *B. triarticulata* (Thomson), *B. fluvialis* Henry, *B. hamata* Brehm (a New Zealand endemic) and *B. robusta* Sars all of which differ very significantly from *B. timmsi*. The latter lacks the large teeth attached to the inner distal corner of the left B2 and the relatively much longer left Re1 found in *B. triarticulata* and *B. fluvialis*. The left Re1 of *B. timmsi* is relatively much shorter than that in *B. hamata* and *B. robusta*, being more comparable with that in *B. symmetrica* Sars.

The question of the taxonomic value of the size and shape of any posterior "wings" developed from the last prosomal segment of female boeckellas is a somewhat vexed one. In some limnetic species they seem not to occur and in others, such as *B. propinqua* Sars, they are clearly subject to a large amount of intraspecific variation (*cf* Bayly 1962b, Fig 18). On the other hand, in species associated with shallow bodies of temporary water such as *B. saycei* Sars, *B. nyoraensis* Searle and *B. bispinosa* Bayly these lobes seem always to be large and of some taxonomic importance (*cf* Bayly 1979, Figs 5C and 6A,C). The large prosomal lobes of *B. timmsi* and the shallow, temporary nature of its habitat are in agreement with this pattern. The extreme shallowness of its habitat, together with its robust body form and relatively short antennules, suggest that this species may be fundamentally littoral or benthic in its habits (*cf* Timms 1979). This species came from a large (4 ha), very shallow (< 40 cm deep) and highly turbid (turbidity 6000 FTU) claypan that contained fresh water (K_{25} 430 µS cm^{-1}).

Derivation of specific name: Named for noted Australian limnologist B V Timms, who collected this new species and drew it to my attention.

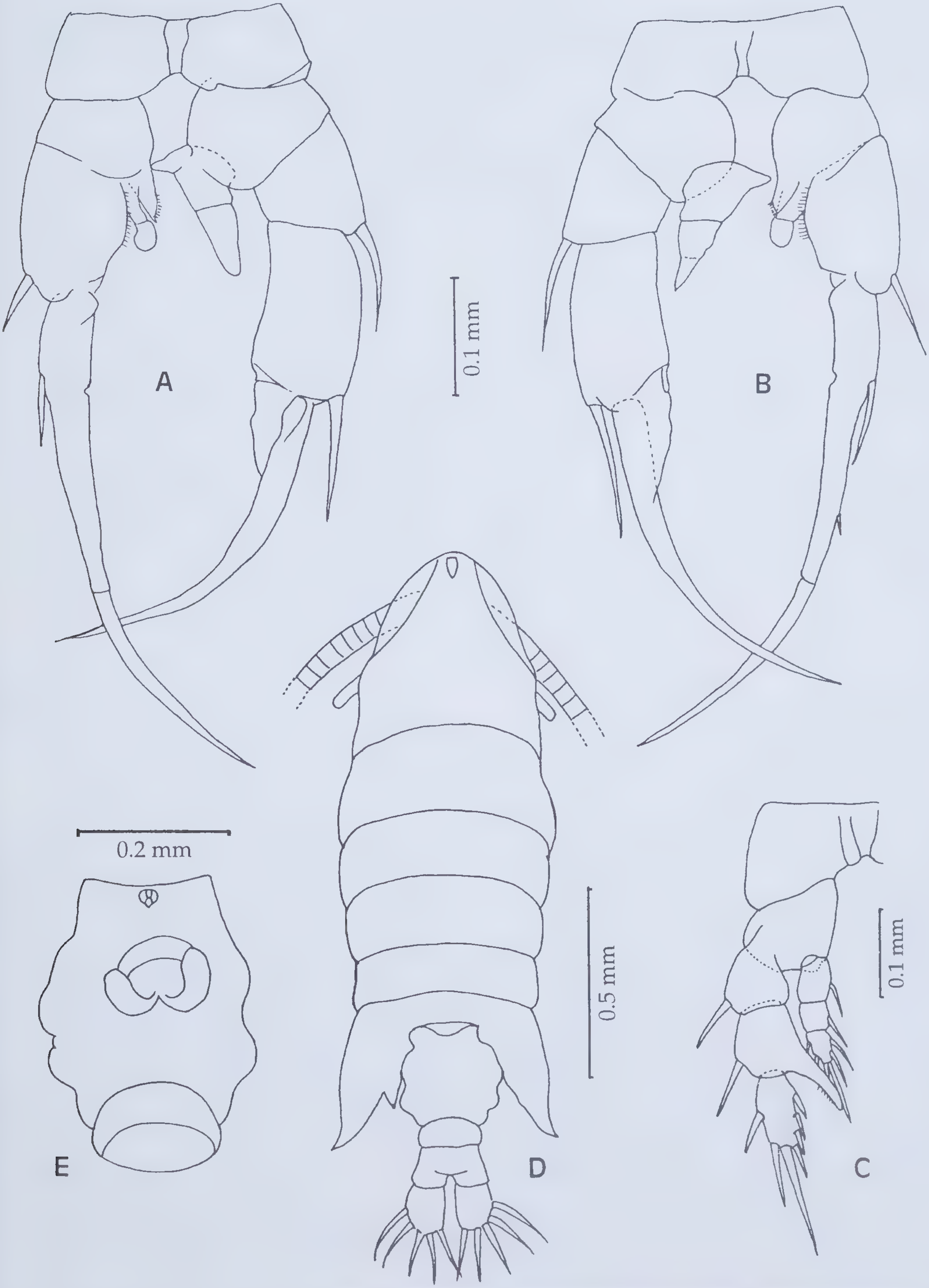

Figure 2. *Boeckella timmsi* sp nov; **A** & **B**, posterior and anterior aspects, respectively, of male fifth legs; **C**, leg of female fifth pair; **D**, dorsal aspect of female (excluding most of antennules); **E**, ventral aspect of female genital segment (plus urosome segment 2).

Acknowledgments: I thank S A Halse and B V Timms for providing me with the material on which this paper is based. It is to the credit of both of them that, on the basis of their own preliminary observations, they thought that they were in possession of a new species. I am indebted to C Petersen and C Logan for producing the typescript.

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Natural history of thorny devils *Moloch horridus* (Lacertilia: Agamidae) in the Great Victoria Desert

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Abstract

Daily movements and activity of three male and five female thorny devils (*Moloch horridus*) were monitored using biotelemetry in the Great Victoria Desert during September, October and November 1995. Both males and females moved up to 200–300 m daily, with males averaging linear daily distances twice as great as those of females (66.6 m *vs* 31.7 m, respectively). Considerable individual variation in movements is evident among thorny devils. Activity does not appear to be confined to a specific area during the mating season (early spring, August–September). Lizards were considerably more active during early spring (September–early October) than in late spring-early summer (late October–early November). This seasonal activity pattern is reflected in burrow usage which increased significantly during late spring. Males and females were active with similar frequencies. Evidence for *M. horridus* navigating by methods other than sight or smell of another conspecific lizard is presented. Colour correlates positively with activity level ($r_s = 0.45$; $P < 0.0001$), with lighter skin colour associated with higher activity levels. Activity level is correlated with both air temperature and sand temperature ($r_s = 0.263, 0.254$; $P < 0.0035$). Colour is also positively correlated with sand temperature ($r_s = 0.256$; $P < 0.0016$) but not with air temperature. Lizards observed feeding in the morning (before 11 am) were dark in colour and lizards feeding in the afternoon (3 to 6 pm) were light in colour. Foraging behaviour was never observed during about (11 am to 3 pm). Thorny devils undergo rapid weight changes that are not related to oviposition. Fat bodies of females are largest during winter, whereas those of males are largest in summer.

Introduction

Foraging behaviour of lizards is correlated with their morphology, ecology and reproductive characteristics, suggesting an evolutionary relationship among these parameters (Vitt & Congdon 1978; Huey & Pianka 1981; Pietruszka 1986; Perry & Pianka 1997). *Moloch horridus*, the thorny devil, exhibits a bimodal seasonal pattern of activity, with almost no movement during the coldest and hottest months of the year (June and July; January and February) and increased activity during the remaining eight months with mating occurring during spring (Pianka & Pianka 1970). Thorny devils live from six to twenty years (Pianka & Pianka 1970). Additionally, these lizards have a highly specialised diet, consisting almost exclusively of *Iridomyrmex* ants (Pianka & Pianka 1970; Withers & Dickman 1995). Other agamids in the same habitats, for example *Ctenophorus isolepis* and *Ctenophorus inermis*, are more generalised feeders, are active year round, and *C. isolepis* might have a yearly adult turnover (Pianka 1971a,b). Thorny devils are morphologically and ecologically more similar to the North American iguanian *Phrynosoma* than they are to other Australian agamids (Pianka 1994a). *Moloch* and *Phrynosoma* have undergone convergent evolution and are ecological equivalents (Pianka 1994a, 1997).

Aspects of behaviour and skin colour of *M. horridus* were studied in the Great Victoria Desert during spring to augment our understanding of this unique agamid. Drinking behaviour has previously been documented (Bentley & Blumer 1962; Withers 1993; Sherbrooke 1993). For a century, data have been presented on the number and type of ants consumed daily by *M. horridus* (Saville-Kent 1897; Davey 1923). Little has been reported on the time of day that thorny devils feed in their natural habitat and their corresponding body temperature, or on dynamics of weight gain and loss. Individual thorny devils can vary their colour from light yellow and brown to dark olive gray and brown. Colour changes, which can be rapid, appear to be associated with body temperature, activity level, and camouflage.

We undertook a radiotelemetric study to deduce whether movements of thorny devils were confined to a discernible activity area from mid-September to early November in the Great Victoria Desert (late spring to early summer). Movements were assessed in relation to burrow usage and location. Daily data were collected to identify distance traversed, microhabitats selected, and individual activity level; these were compared with observed skin colouration, time of day and ambient temperature conditions (substrate and air).

Methods

Eight *M. horridus* were located by following their spoor in the sand of the Great Victoria Desert (28° 12' S, 123° 35' E), captured and fitted with external transmitters, each emitting a unique, rhythmic signal (Biotelemetry Tracking, South Australia). Animals were sexed by external appearance (males have a much more bulbous tail base than females). Lizards were measured, weighed, and assigned an alphabetic character for identification.

Between 100 and 200 sets of observations were made during a two month period (mid-September to early November 1995) with 1–2 sets of observations taken each day. Observations were made at different times of day to increase the diversity of activity information. Observers approached the last recorded location of each lizard slowly and quietly, and tried to locate the animal visually before using the audio assistance of the transmitters and a tuned receiver, to minimise interruption of the thorny devil's daily routine. However, in some cases the lizard had clearly noticed the observer before any information on position, activity and/or colour could be recorded.

Each lizard's position was identified at each sighting by triangulation from compass bearings to two of more than a dozen elevated markers. For each position, observations of activity level, colour, nearest foliage, and exposure to the sun were recorded each day. Ambient air temperature and surface sand temperature (in shade or sun, depending on the location of the individual), time of day, and proximity to a burrow were also noted. Ambient temperature was measured daily at 9 am at the Yamarna weather station (Bureau of Meterorology, Perth), located about 8 km northeast of the study site.

Daily positions were plotted for each lizard on an overlay of an aerial photograph of the study site. Points were converted into x and y coordinates for each individual to produce an image of the course and direction of movement. Active and non-active days, total movement, daily linear movement, average daily movement, and maximum daily movement were calculated for two subdivisions of the study period [period A, early spring, 14 September to 20 October; period B, late spring-early summer, 21 October to 8 November] which reflected distinct changes in activity level to further elucidate seasonal changes in movement patterns.

Lizard colour, activity level, temperature, sun/shade exposure and time of day were graded numerically. Activity levels were graded as prostrate (1), upright (2), moving (3), and burrowing (4). Sun exposure was categorised as in full sun (1), in partial sun (2), in shade (3), exposed but cloudy (4) and in burrow (5). Colour descriptions were recorded as dark olive brown (1), olive brown (2), light olive brown (3), yellow (4), or very light yellow (5), although this colour gradient is actually continuous. Temperature and time of day were treated as continuous variables. Data were analyzed using non-parametric Spearman rank correlation coefficients, corrected for ties in temperature or time of day.

In addition to data we collected on these eight individuals, we also report substantial other information collected by ERP over the interval from 1966–1993 at various localities in the western Great Victoria Desert (for dates and localities, see Pianka 1969, 1986, 1994b; Pianka & Pianka 1970); these data include ambient temperature, body temperature, color, and fat body size. For each lizard collected, color was recorded along with body temperature (taken with a thin-bulb Schultheis mercury thermometer) immediately upon capture. Ambient air temperatures were measured at about 1 m above ground. Lizards were dissected in the laboratory and lengths of fat bodies measured to the nearest mm.

Results and Discussion

Dates of capture, weights, snout-vent length (SVL) and sex of lizards monitored are presented in Table 1. Sexual dimorphism is apparent, with females being larger and stouter (Pianka & Pianka 1970). Females averaged 45.5 g (± se 5.2) in body mass and 91.0 mm (± se 3.6) in SVL. Males were considerably smaller, with an average body mass of 31.2 g (± se 1.3) and SVL of 78.7 mm (± se 1.8).

Table 1

Identification letter (ID), date of first capture, sex, snout-vent length (SVL), and weights of thorny devils monitored in this study.

ID	Date	Sex	SVL (mm)	Weight at first capture (g)	Weight on 8 Nov, 1995 (g)
M	14 Sept.	♂	82	33.0	(lost 6 Oct)
N	15 Sept.	♀	105	57.0	46.5
O	20 Sept.	♀	88	38.9	49.5
P	27 Sept.	♀	85	28.5	(lost 31 Oct)
Q	27 Sept.	♀	87	52.0	42.5
R	28 Sept.	♂	76	28.5	30.0
S	4 Oct.	♂	78	32.3	(lost 12 Oct)
T	5 Oct.	♀	90	51.0	48.5

Body weight changes

Moloch appear to gain and lose weight quickly. Although we were reluctant to weigh our study animals routinely for fear of disturbing their behaviour, we did document some substantial changes in body mass (Tables 1 and 2). Five lizards were weighed both at capture and at the conclusion of this study (Table 1). The single male (R) gained 1.5 g in 41 days (+5.3 % of initial body mass). Two gravid females (N and Q) lost weight after oviposition and then regained some weight (Table 2) for large overall losses in body mass (-18.4 % and -18.3 % respectively). Another female (O) that did not oviposit gained 10.6 g in 51 days (+27.2 %) (Table 2). Female T did not oviposit but lost 2.5 g in 33 days (-4.9 %). We documented rapid body weight gain following rain by female O. This lizard weighed 40.0 g on 27 September but after a night of rain (on 28 September) it weighed 41.75 g (a one-day weight gain of 1.75 g or +4.4 %, presumably by water absorption). As discussed above, two other females (N and Q) which oviposited on 20 September and 3 October, respectively, were each weighed several times during the course of our study

Table 2

Weights of three female thorny devils on different dates during the study period.

Date	Weight (g)
Female N	
15 Sept	57.0
19 Sept	62.5 (+9.6%)
20 Sept	37.5 (-40.0%)*
8 Nov	46.5 (+24%)
Female O	
20 Sept	38.9
27 Sept	40.0 (+2.8%)
28 Sept	41.75 (+4.4%)
8 Nov	49.5 (+18.6%)
Female Q	
27 Sept	52.0
3 Oct	30.3 (-41.7%)*
8 Nov	42.5 (+40.3%)

* Body weight reductions attributed primarily to observed egg laying

and their body weights fluctuated considerably (Table 2). Each of these gravid females regained considerable body weight rapidly following oviposition (+24 % and +40 %).

Daily and seasonal movements

Average and maximum daily movements for each lizard were calculated (Table 3). Movements were calculated as being linear between successive locations but are therefore underestimates of actual distance moved since lizards usually moved in a non-linear fashion. One male thorny devil (S) was observed for only 8 days before it was lost; it was in or next to its burrow during this time, and therefore it is not included in Table 3. Individual thorny devils differed considerably in the extent of movement; for example, ♂M and ♀N both moved over 1400 m during the study, whereas others moved less than 1000 m.

Table 3

Daily movement parameters of thorny devils divided into two periods; A = Sept 14 to Oct 20; B = Oct 21 to Nov 8. Total distance moved represents a minimal estimate, as indicated in the text. Average daily distance moved is mean ± se.

	Observation period	Total distance moved (m)	Average daily distance moved (m)	Maximum daily distance moved (m)
♂M	A	1436.9	110.5 ± 59.0	310.0
♀N	A	1666.0	47.6 ± 11.0	245.1
♀N	B	44.4	2.5 ± 0.9	12.0
♀O	A	257.3	8.8 ± 2.8	70.3
♀O	B	20.1	1.3 ± 0.5	25.0
♀P	A	312.7	13.6 ± 3.2	59.6
♀P	B	77.5	7.8 ± 3.0	25.1
♀Q	A	827.7	36.0 ± 11.6	177.6
♀Q	B	162.0	9.0 ± 2.0	19.4
♂R	A	1127.9	51.3 ± 10.4	148.0
♂R	B	55.8	2.9 ± 1.1	16.1
♀T	A	294.0	22.6 ± 8.6	102.1
♀T	B	135.6	7.5 ± 2.8	42.8

Table 4

Sexual differences in average daily (mean ± se) and maximum distances travelled by thorny devils observed over the entire period of this study.

Sex	N (days)	Average daily distance moved (m)	Maximum daily distance moved (m)
males	36	66.6 ± 13.3	310.0
females	211	31.7 ± 2.6	245.1

Although movement of individuals varied considerably, data for males and females were compared. Male thorny devils, on average, travelled twice as far in a day as females. Additionally, the longest distance moved in one day by a male (310 m) was 65 m further than the maximum travelled by any female (Table 4). Over the entire period of the study, males moved a greater average daily distance than females ($t_{12} = 3.08$; $P = 0.0095$ as well as greater maximal daily distances ($t_{12} = 3.48$; $P = 0.0046$). Males also moved a greater distance than females during the the early spring period (average daily distance, $t_6 = 3.04$, $P = 0.0229$; maximal daily distance, $t_6 = 4.48$, $P = 0.0042$), but the sample size was too small for testing significance of differences during late spring-early summer. Comparison of all lizards of both sexes for early *vs* late seasons also shows a longer movement during the early spring than in late spring ($t_{12} = 3.1$; $P = 0.009$).

Differences between total days active and inactive for males and females during both periods, compared using contingency table analyses (Table 5), indicate that male activity did not differ from that of females within the two time periods (early and late spring; $\chi^2 = 0.00013$ and 0.00025; $P > 0.8$). However, a distinct shift in behaviour was noted between time periods. Movements of both sexes were more frequent during early spring than late spring ($\chi^2 = 17.88$, $P < 0.0001$). Activity changes cannot be attributed to changes in ambient temperature since the difference between average temperatures at 9 am (the only consistent daily temperature measurement made at Yamarna) for the two periods is not significant ($t_{55} = 0.23$). Similarly, average minimum temperatures for each period did not differ significantly ($t_{55} = 0.003$). Inactive days were spent either in shallow burrows or in the shade of a small shrub.

Movements overlain on an aerial photograph of the study area (Fig 1) show that thorny devils. ♂M and ♀N moved over much greater distances than the other thorny

Table 5

Male and female activity (days) given separately for males and females in observation periods A (Sept 14–Oct 20) and B (Oct 20–Nov 8), and combined data for males and females.

	Period A		Period B		Males and Females	
	Male	Female	Male	Female	Period A	Period B
Active	30	84	8	39	114	47
Inactive	13	39	12	52	52	64
% Active	69.8^{a}	68.3^{a}	40.0^{b}	42.9^{b}	68.7^{a}	42.3^{b}

^{a,b} frequencies with same superscript do not differ significantly.

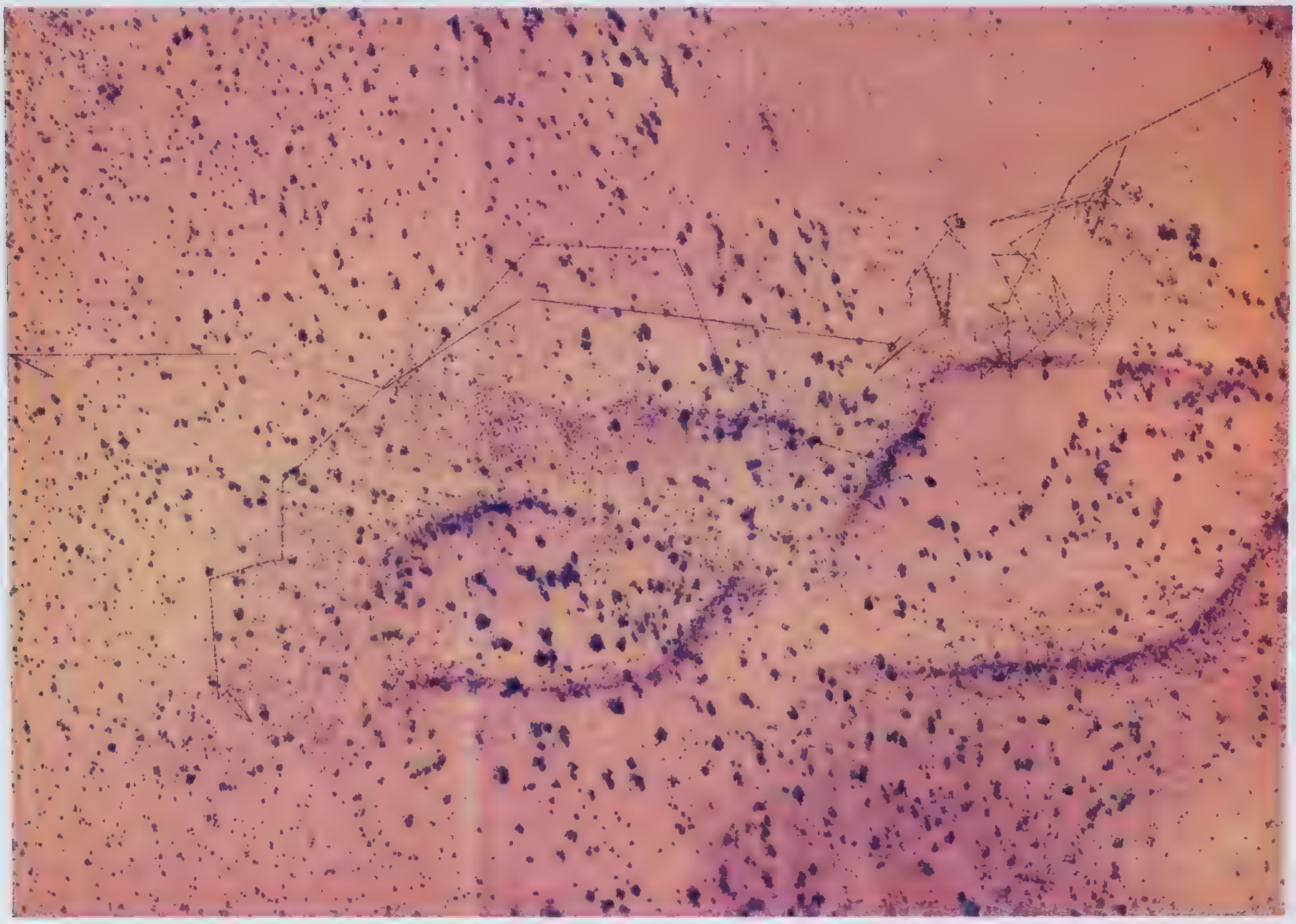

Figure 1. Movements of eight *Moloch horridus* individuals in sandridge habitat of the Great Victoria Desert, between 14 September and 8 November 1995.

devils. No defined activity area was observed for lizards ♂M, ♀N, ♀O, ♂R, or ♀T. Although ♀P repeatedly returned to the same area, its behaviour was anomalous within the context of the study. With more extended study, the relationship between the bimodal seasonal pattern of activity and movements of *M. horridus* might reveal a defined activity area during part of the year.

If the Australian thorny devil has an evolutionary history parallel to its American counterpart, the Texas horned lizard (*Phrynosoma cornutum*), then *M. horridus* might also have shifted away from a strict home range (such as by the agamids *Ctenophorus fordi* and *Ctenophorus isolepis*) towards semi-nomadic behaviour. Guyer (1991) presents two arguments for this shift among *Phrynosoma*, both of which could apply to *M. horridus*. First, the behaviour to freeze rather than run and hide eliminates the need for planned escape routes; and, second, the strict diet of ants might require nomadic movement to follow shifting ant activity patterns (Baharav 1975; Munger 1984). Non-nomadic aspects of behaviour of *M. horridus* might be related to mating rather than evasion of predators (except in the case of gravid females, see discussion on burrow usage) or feeding requirements.

Thorny devils appear to have a navigational ability that cannot be attributed solely to visual recognition or olfactory detection of conspecifics. Although Sporn (1955) described the ability of the thorny devil to perceive flying birds at a long distance, Tollestrup (1983) noted that small lizards are often unable to attain the height necessary to observe others of their species. However, thorny devils might well be able to navigate known terrain by visually locating a specific landmark (*e.g.* a tall shrub). Pianka & Pianka (1970) report finding four thorny devils (two males and two females; individuals of each sex differing in size) at the base of the same large shrub in the early spring on 25 August, 1967 (Fig 2). Such an aggregation of thorny devils had never been previously reported. Winds had erased all tracks the day before. These four thorny devils were back-tracked for varying distances (40–120 m). Two males approached the shrub from the south and south-west at a 90° angle to the path of approach of the larger female, which came in from the east. The smaller female came from the south-west, crossing over the track of the medium-sized male and went to a *Hakea* bush that was also visited by the larger female. Since these lizards converged from 90° compass directions, scents carried by prevailing winds could not have been the primary means by which they navigated. They were also definitely not following tracks of a prospective mate, as we have observed for another local desert lizard, *Varanus tristis* (Thompson *et al.*, in press). We are inclined to interpret this event as a mating rendezvous.

Burrow usage

Oviposition burrows terminate as an air-filled

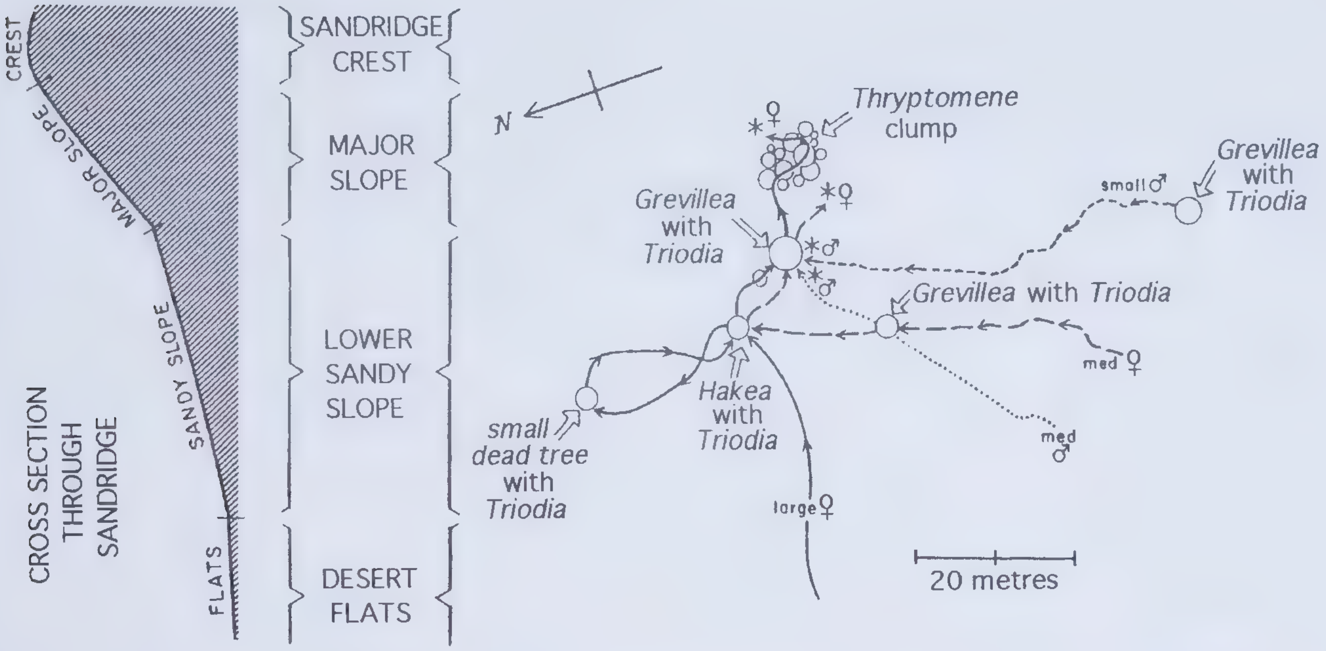

Figure 2. Movements of four thorny devils, two males and two females at a study site near Lorna Glen, Western Australia, on 25 August 1967. Strong winds erased all tracks the day before. These four lizards were of different sizes, allowing each individual to be back-tracked for varying distances to establish their movements.

chamber about 8–9 cm high by 10–12 cm wide and about 12–15 cm long, about 20–22 cm below the surface, which is large enough to accommodate several adult thorny devils (Pianka *et al.*, 1996). Non-oviposition burrows are much shallower and smaller than oviposition burrows (only 5–10 cm deep and about 5x5x10–12 cm, just large enough for a single thorny devil). The three male thorny devils (M, R, and S) each frequented only a single burrow during the study period. Females N and Q were gravid at the time of capture and laid their eggs during the observation period. Lizards ♀N and ♀Q occupied non-oviposition burrows after deposition of their eggs where they remained three to four times longer than they had stayed in their oviposition burrows (Table 6). Oviposition burrows and post-oviposition burrows were at opposite extremes of their observed activity areas. Non-gravid females (♀O, ♀P, and ♀T), although they had no oviposition burrows, also spent more time in their later burrows (Table 6). After mid-October, the single remaining male and four females spent much longer times at the same burrows (Table 6). Pianka & Pianka (1970) suggested that *M. horridus* increases movement (reduces time spent in burrows) in early spring to increase the chance of encounters between prospective mates.

Table 6

Burrow use by *M. horridus* (italic entries denote oviposition burrows). Different dates/durations for individuals indicate different burrows are used.

	Date of initial occupation (D/M/Y)	Duration of Occupation (days)
♂M	17/9/95	1
♀N	*16/9/95*	5
	24/9/95	3
	16/10/95	2
	25/10/95	14
♀O	20/9/95	2
	16/10/95	16
♀P	11/10/95	1
	16/10/95	3
♀Q	*29/9/95*	6
	12/10/95	4
	16/10/95	18
♂R	10/10/95	14
♂S	10/10/95	2
♀T	15/10/95	4
	19/10/95	10
	29/10/95	18

These temporal and spatial patterns suggest that the large scale movements of *M. horridus* might not be random. The 1967 event depicted in Fig 2 occurred in August, just before the calender month in 1995 when multiple gravid females were collected. In 1995, thorny devils were never sighted together and aggregates in this species are rare (Pianka & Pianka 1970; Withers & Dickman 1995). Although *M. horridus* has a life span of six to twenty years (Pianka & Pianka 1970), long term movement data are scarce. Withers & Dickman (1995) report that eight individuals remained within 100 m of the same location after six months and that one had moved 2.5 km after four years. These movements might reflect seasonal mating behaviour, possibly involving long forays to ensure a meeting with other thorny devils and/or a seasonal return to a specific activity area. Since our study period was restricted to late spring, no definitive statements can be made regarding the extent of nomadism present in movements of *M. horridus*.

Thermoregulatory behaviour

Colour is strongly and positively correlated with

Table 7

Correlation analyses of behavioural response to environment in *M. horridus* (r_s = Spearman rank correlation coefficient corrected for multiple ties; n = number of observations; P = probability of obtaining this level of correlation by chance; NS = not significant).

	r_s	n	P
colour *vs* sand temperature	0.256	153	<0.0016
colour *vs* air temperature	0.139	154	0.0867 (NS)
colour *vs* in sun/shade	-0.110	149	0.1807 (NS)
colour *vs* time of day	0.135	167	0.0839 (NS)
colour *vs* activity level	0.450	136	<0.0001
activity level *vs* sand temp.	0.254	135	<0.0035
activity level *vs* air temperature	0.263	136	<0.0023
activity level *vs* in sun/shade	-0.031	141	0.7161 (NS)
activity level *vs* time of day	-0.120	160	0.1301 (NS)

activity level, indicating that skin colour lightens as activity increases (Table 7). Colour is also positively correlated with sand temperature, with lighter colour at a higher ambient substrate temperature (Table 7). However, colour appears to be independent of sun exposure, air temperature and time of day (Table 7).

The chameleon-like ability of *M. horridus* to change skin colour, thus blending in with surrounding leaf litter, has been known for many years (White 1947; Pianka & Pianka 1970) and was frequently observed during the course of our study, often making it almost impossible to visually locate the transmitting lizards. Data collected by ERP from 1966 to 1992 reveal that although thorny devils can have a high body temperature when dark coloured, they are less likely to be yellow at low body temperatures (Fig 3). The lowest body temperature recorded for a yellow thorny devil was 27.5° C, which is 3.1° C higher than the lowest recorded body temperature for a dark coloured thorny devil.

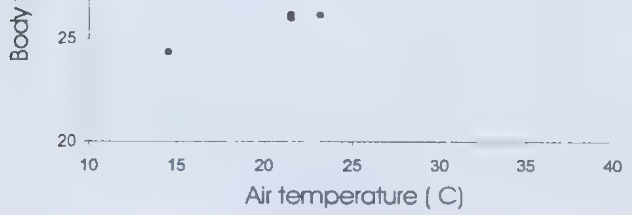

Figure 3. Relationship between body temperature and ambient air temperature for *Moloch horridus* with light (open symbols) and dark (closed symbols) body colour. Least squares regression line for light-coloured lizards is significantly higher than for dark-coloured lizards (ANCOVA; $F_{1,62} = 16.6$, $P < 0.0001$; slope $t_{62} = 0.71$, $P > 0.50$, NS; elevation $t_{63} = 7.45$, $P < 0.001$). Regression equations relating body temperature to ambient air temperature (T_a; °C) are for dark colour (——; $T_b = 21.89 + 0.371\ T_a$; $r^2 = 0.34$) and for light colour (— — —; $T_b = 26.97 + 0.261\ T_a$; $r^2 = 0.16$).

Correlations between air temperature and body temperature have previously been reported for thorny devils (Pianka & Pianka 1970, r = 0.625, P<0.01; Withers & Dickman 1995). Individuals were frequently observed flattened against the sand, maximizing contact between body and sand. They were also observed standing on their hind legs, with front legs supported on a shrub. Withers & Dickman (1995) reported that thorny devils can use this posture when eating ants; we also observed thorny devils in this position when no ants were visible. Based on these observations and the correlation between air and body temperature, *M. horridus* does not appear to be a passive thermoconformer, but basks (is heliothermic) and may use contact with the sand (is thigmothermic) to regulate its body temperature.

Foraging behaviour

Thorny devils are classic "sit-and-wait" predators (Pianka 1966; Perry & Pianka 1997), although they probably select their feeding sites with care. Thorny devils were observed feeding only during the morning before 11 am and afternoon between 3 and 6 pm. In the morning, all twenty foraging individuals were various shades of olive/brown. In late afternoon, the three foraging thorny devils were light yellow. Of 46 observations on thorny devils made between 11am and 3pm, none were feeding. Consumption of ants was recorded only when animals were near a *Triodia* tussock or *Thryptomene* shrub and when sand temperatures were at least 24° C and occasionally above 40° C. Ants might be consumed independently of body temperature with use of camouflage darkening tactics complicating our observations.

Fat stores

Like many lizards, *Moloch horridus* stores lipids in paired fat bodies that protrude into the postero-ventral body cavity. Fat body lengths for a large series of thorny devils collected at various times of the year (measured by ERP) show that fat body cycles differ for males and females. Female thorny devils have a seasonal variation in fat body sizes, with smaller fat bodies during summer and larger fat bodies in winter (Fig 4, lower panel), but no such trend is evident among male thorny devils (Fig 4, upper panel). This sex-specific difference is probably a direct consequence of oviposition by females. To produce a clutch of eggs in the early spring, females must mobilize their fat reserves, which are then replenished during autumn.

Conclusions

This study emphasises the usefulness of colour in indicating behaviour patterns of thorny devils. The colour of a thorny devil colour reflects its activity level unless the lizard has darkened its skin and crouched in the leaf litter or shade, presumably to elude a potential predator. These lizards appear to be both heliothermic (sun bask) and thigmothermic (adjust their body contact with the sand) to regulate their body temperature. Further and more detailed studies with

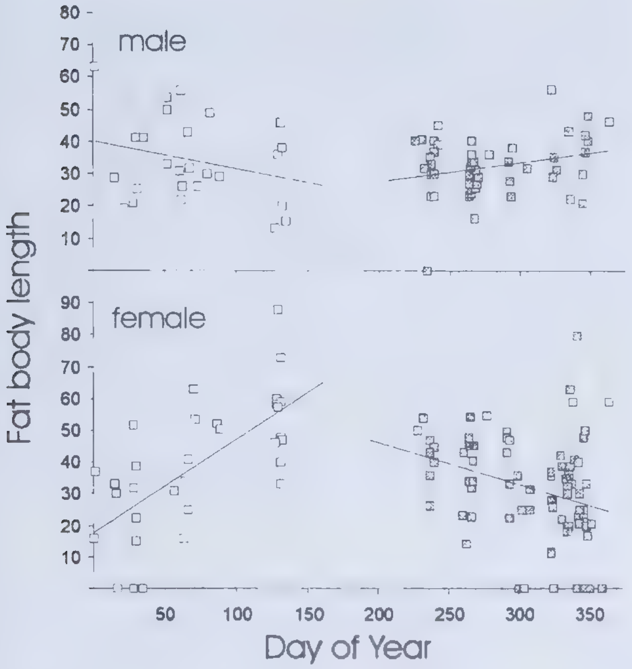

Figure 4. Annual cycle of fat body lengths for male (top) and female (bottom) thorny devils (1 = Jan 1 and 365 = Dec 31). Raw data (the sum of lengths of both fat bodies for each lizard) are plotted for each lizard (two data points are coincident for a few values). Least squares linear regressions fitted to data for the first half and second half of the year are also shown. Slopes for males and females are opposite in sign and significantly different (tests of parallelism; first half year, $F_{1,56} = 18.58$, $P < 0.000067$; second half year, $F_{1,130} = 9.93$, $P < 0.002$). Regression equations (coefficients significantly different from zero are shown in boldface type); early males, $y = 39.84 - 0.084x$ ($r^2 = 0.027$; $P = 0.2002$); early females, $y = 17.475 + 0.298x$ ($r^2 = 0.452$; $P < 0.0001$); late males, $y = 11.494 + 0.072x$ ($r^2 = 0.069$; $P = 0.0317$); late females, $y = 70.78 - 0.125x$ ($r^2 = 0.071$; $P = 0.0093$).

multiple daily body temperature measurements of individual lizards in a natural environment are needed to confirm this suggestion.

Thorny devils were never observed to feed in mid-day during spring. The majority of thorny devils that were observed to forage were feeding in the morning and were a dark color (indicative of either a low body temperature or active camouflage). Feeding could be independent of body temperature, but further studies of natural foraging behaviour and concommitant body temperature are needed to clarify this relationship.

In a natural environment, thorny devils can gain and lose weight rapidly. Large weight changes accompany oviposition as noted previously (Pianka *et al.* 1996), but here we report substantial, non-ovipositional weight changes over variable time periods. Fat body cycles differ between the sexes, probably because females must invest lipids in egg production during early spring. Additional field work is needed to (1) record rates of weight gain and loss, (2) measure the percentage of weight gain due to water absorption and/or ant consumption, and (3) to interpret the functional significance of these rapid changes in body weight.

Thorny devils can travel long distances (up to 200–300 m per day) and undertake such movements in early spring. Seasonal fluctuations in burrow use and daily movements reflect the bimodal annual pattern of activity reported by Pianka & Pianka (1970), further indicating the uniqueness of this agamid. Increased movements may be a part of seasonal mating behaviour governed by visual detection of large landmarks such as shrubs. Patterns of burrow use suggest that gravid female *M. horridus* might travel to a spot away from their non-oviposition burrows to deposit their eggs. Further movement studies are necessary to ascertain whether this species is entirely nomadic, semi-nomadic or maintains a home range. Seasonal data on male and female movements from immediately prior to our study period (August to mid-September) would clarify whether non-oviposition burrows were occupied before egg deposition, which could indicate that they are part of an annually occupied area.

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Distribution and characteristics of mound-building termites (Isoptera) in Western Australia

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Abstract

We review here observations on mound-building in the Western Australian termite fauna, based on published data and the combined unpublished observations of the authors (M A-T 1987 – 1997, D H P 1950s to 1980s). We also examine the extent to which mounds of different species vary in shape and size across their geographic distribution and the major habitats where they build mounds, and give broad guidelines for identification of the mound-builder. Our observations cover all major regions of the State but are least comprehensive for the tropical Kimberley region.

A total of 153 described termite species, from 4 families and 26 genera, are known to occur in Western Australia. Of these, at least 21 species (14 % of species) from two families and seven genera build mounds. Nine species (43 %) are obligate mound-builders. Genera with mound-builders include the rhinotermitid *Coptotermes* (3 spp), and the termitid genera *Amitermes* (2 spp), *Drepanotermes* (6 spp), *Microcerotermes* (2 spp), *Nasutitermes* (2 spp), *Tumulitermes* (5 spp) and *Xylochomitermes* (1 sp). Three mound-building species are widely distributed north and south of the Tropic of Capricorn, seven species are restricted to parts or all of the south-west, three species are largely restricted to the arid centre, four species are largely restricted to the northern half of the State (including the Kimberley), and four species are west-coastal or near west-coastal in distribution. At least five additional species of *Amitermes, Macrognathotermes, Microcerotermes* (2 spp) and *Xylochomitermes* may construct mounds in northern-most Western Australia (Kimberley). Mounds range in height from pavement-like mounds barely rising above the soil surface, to mounds reaching over 4 m in the tropics. Materials used for mound-construction vary from almost pure clay to a mixture of sand and clay, soil and faecal material.

Introduction

Termite mounds (termitaria) are one of the most conspicuous features of many Australian landscapes, particularly in tropical regions which support the tallest of the termitaria (Calaby & Gay 1959; Gay & Calaby 1970; Andersen & Jacklyn 1993). Approximately one-fifth of the described Australian termite fauna construct mounds (Watson & Gay 1991). Mound-building termites often occur in great abundance, and more than 700 active mounds ha^{-1} have been recorded in Australia (Watson *et al* 1973; Spain *et al* 1983; Holt & Easey 1993). Lee & Wood (1971) record 65 tonnes ha^{-1} of above-ground mound material at one site, and estimate some of the mounds of *Nasutitermes triodiae* to weigh > 10 tonnes. In addition to the importance of mound-building termites to many ecological processes such as soil modification (Lobry de Bruyn & Conacher 1990) and energy flows (Abensperg-Traun 1994), mounds also provide important shelter and breeding sites for a considerable diversity of small- and medium-sized mammals, birds, reptiles, frogs, and invertebrates including other termite species (Calaby 1956; Spain & Brown 1979; Braithwaite 1990).

Mound-building (as well as subterranean) termites remain poorly known to most but specialist entomolgists, despite their functional importance and often high visibility over most of inland Australia. The aim of this review is to synthesize current knowledge of the mound-building termite fauna of Western Australia, particularly with regard to their geographic distribution, mound shapes and sizes, and the materials used for mound construction. We also provide guidelines for the identification of mound-building species, as opposed to termite species that inhabit the mounds of mound-builders as obligate or facultative (opportunistic) co-inhabitats.

Observations on mound-building behaviour

Mound-building species were probably amongst the first termites to be described for the Australian region because of the high visibility of most mound-building termites, relative to subterranean species. There are published observations on mound-building behaviour for most species but observations are widely scattered in the literature and they are inconsistent in detail and geographical emphasis. Published as well as unpublished observations contribute to our synthesis. Accumulated field observations from the early 1950s to the late 1980s (D H Perry) cover all parts of the state except the tropical Kimberley region where observations by J A L Watson on mound-building *Drepanotermes* species (Watson & Perry 1981), are used. We incorporate in this review observations on mound-building termites from the Kimberley that were reported elsewhere (*e.g.* Calaby & Gay 1956; Gay & Calaby 1970). Data for the central and southern wheatbelt are from studies of Abensperg-Traun

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and colleagues between 1987 and 1997 (*e.g.* Abensperg-Traun & De Boer 1990; Abensperg-Traun 1992; Abensperg-Traun *et al.* 1996 for the central wheatbelt; Abensperg-Traun & Milewski 1995 for the southern wheatbelt). Data on mound-building *Coptotermes* spp are supplemented by observations in Western Australia by Gay (1955) and Calaby & Gay (1956).

For each mound-building species we provide a map of its broad geographical distribution within Western Australia (from Watson & Abbey 1993), and observations on whether the species is 'obligate' (always builds mounds) or 'facultative' (builds mounds in only part of its geographical range). Mound shapes and common dimensions (height and width at base), the materials used for their construction, and major habitats where the species' mounds occur, are also included. Head-capsule morphology of soldier termites is generally used for species identification, and we provide dorsal views of the soldier caste for each species (redrawn from Hill 1942, Watson & Perry 1981, Perry *et al.* 1985 and Miller 1991).

We group mound-building species into five broad distributional patterns;

(i) species that occur over most areas of mainland Western Australia;

(ii) species largely restricted to parts or all of the south-west, arbitrarily defined by the 250 mm rainfall isohyet which incorporates all of the wheatbelt and eucalypt forests;

(iii) species largely restricted to the inland areas of the arid region (broadly delineated by the 250 mm rainfall isohyet north and south of the Tropic of Capricorn);

(iv) species occurring over most parts of the region north of the Tropic of Capricorn (but that are largely absent from the southern half of the State); and

(v) species restricted to coastal or near-coastal areas within any one of the above distributional categories.

Mound-building species

Of the 153 described termite species from 26 genera and four families known to occur in Western Australia (extracted from Watson & Abbey 1993), at least 21 species (14 %) from two families and seven genera are known to build mounds (Table 1). Nine species (43 %) are obligate mound-builders.

Widely-distributed species

• ***Coptotermes acinaciformis*** (Rhinotermitidae; obligate; Fig 1) is common in vegetation dominated by *Eucalyptus* but is generally absent where there are no eucalypts.

Table 1

Numbers of described termite species known to occur in Western Australia, numbers of Western Australian species known to build mounds, and additional species likely to construct mounds in the tropical north (see text). * = extracted from Watson & Abbey (1993). Number of obligate mound-builders are shown in parentheses

Family/*genus*	Total number of species*	Number of species known to build mounds	Number of additional species that may build mounds in the tropical north (Kimberley)
Mastotermitidae			
Mastotermes	1	0	0
Kalotermitidae			
Bifiditermes	1	0	0
Cryptotermes	3	0	0
Kalotermes	2	0	0
Rhinotermitidae			
Coptotermes	5	3 (2)	0
Heterotermes	8	0	0
Schedorhinotermes	4	0	0
Termitidae			
Ahamitermes	2	0	0
Amitermes	48	2 (0)	1
Apsenterotermes	3	0	0
Cristatitermes	4	0	0
Drepanotermes	20	6 (3)	0
Ekphysotermes	3	0	0
Ephelotermes	3	0	0
Hapsidotermes	1	0	0
Hesperotermes	1	0	0
Incolitermes	1	0	0
Lophotermes	2	0	0
Macrognathotermes	3	0	1
Microcerotermes	7	2 (0)	2
Nasutitermes	8	2 (1)	0
Occasitermes	1	0	0
Occultitermes	2	0	0
Paracapritermes	1	0	0
Tumulitermes	14	5 (3)	0
Xylochomitermes	5	1 (0)	1

Mounds are "lean-to" slab nests of clay, usually up to ≈ 50 cm high (Fig 1, Plate 1). Mound/nest surfaces are characterized by an irregular network of superficial cracks which is typical for the clay-rich mounds/nests of *Coptotermes* species in general. Nests are commonly established around a fire scar at the base of eucalypt trees which provides access to the heartwood (as opposed to sapwood) upon which the species feeds. Such nests may also be built entirely on the inside of the tree, but with little or no external evidence. The heartwood of trees is progressively eaten out by the termites and is replaced by clay 'pipes' which run up the main trunk and may eventually penetrate all limbs and branches (Greaves 1962; Perry *et al.* 1985). This action creates the hollow trees and logs upon which a great variety of Australian birds and mammals depend for shelter and breeding (Saunders *et al.* 1982; Abensperg-Traun & Smith 1993). Where the host tree has collapsed (*e.g.* storm damage), nest reconstruction around the remaining stump may result in a broadly conical mound form up to ≈ 1.5 m in height. Less commonly, mounds may have no stump or wood inside them. Only one such mound has been recorded for the central wheatbelt (117° 45' E, 31° 24' S), for example, with a height and width at the base of 89 cm and 95 cm, respectively. Nest/mound walls are of clay; they may be 30-50 cm thick and are extremely hard (Calaby & Gay 1956; Perry *et al.* 1985). A single colony may contain well in access of one million individuals (Greaves 1967).

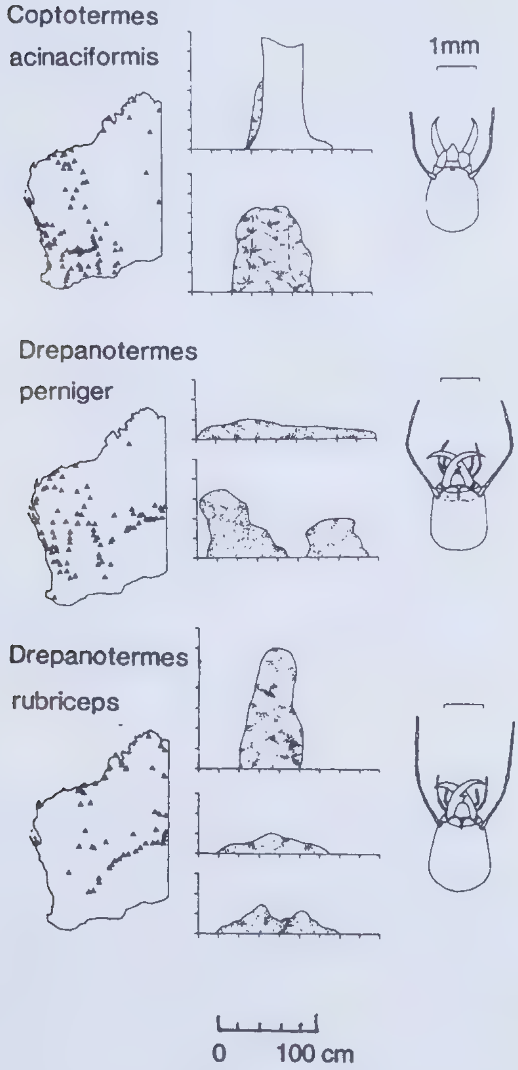


Figure 1. Western Australian mound-building termite species with a state-wide distribution, common mound shapes and dimensions, and a dorsal view (and dimension) of soldier head-capsules for respective species.

- ***Drepanotermes perniger*** (Termitidae; facultative; Fig 1) inhabits a wide variety of habitats; it can be locally common but is largely absent from heath/shrubland (on very sandy soils) and from forested (higher rainfall) areas of the south-west. Mounds are a mixture of sand and clay and are of variable shapes, flat and pavement-like to ≈ 20 cm high and ≈ 3 m wide, or broadly conical and irregular, to 1.5 m high and wide. Pavements are commonly ≈ 20 cm high but may be level with the surrounding soil surface and mound caps are several centimetres thick. Individual colonies frequently construct more than one mound to accommodate the growing colony (Holt & Easey 1985). Watson *et al.* (1973) estimate that moderately-sized colonies may contain ≈ 20 000 individuals. Population build-up of the species, particularly that expressed in the construction of new mounds, has been shown to correlate with long periods (years) of above-average rainfall, with an estimated longevity of individual mounds of up to 250 years (Watson *et al.* 1988). Mound construction following good years may result in up to 20% of the soil surface covered by the hard pavement-like mound surfaces which resist erosion and plant establishment, resulting in significant, detrimental and long-term effects on ecosystem function (Watson & Gay 1970; Watson *et al.* 1973). Mound-building does not occur, for example, in the central and southern wheatbelt but predominates in central parts of its Western Australian distribution. *Drepanotermes perniger* also takes over the mounds built by other species of *Drepanotermes* (Watson & Perry 1981).

- ***Drepanotermes rubriceps*** (Termitidae; obligate; Fig 1) is commonly associated with species of spinifex (hummock grass) of the genera *Triodia* and *Plectrachne* in mulga lands (Watson *et al.* 1973) but inhabits a range of habitats across large areas of the state. It is absent from the forested (higher rainfall) areas of the extreme south-west and extends slightly further into the central wheatbelt of the south-west (*e.g.* Kellerberrin, 31° 38' S, 117° 43' E) than is shown by Watson & Abbey (1993). In the central wheatbelt it is restricted to heath/shrublands on sandy soils where it can be particularly common in heath dominated by the sedge *Ecdeiocolea monostachya*. Mounds are of sand and clay, low and broadly rounded to a maximum height of ≈ 30 cm (arid regions), or flat, pavement-like averaging ≈ 20 cm in height (central wheatbelt). Pavement mounds may be covered by loose soil and are then difficult to detect. In the Kimberley region, mounds may be taller, as high or higher than wide, and are sometimes built in areas subject to seasonal flooding (Watson & Perry 1981). Mound densities of ≈ 200 mounds ha^{-1} have been recorded. *Drepanotermes rubriceps* also takes over the mounds of other species, and then modifies their internal structure (Watson & Perry 1981). Individual colonies may construct several mounds (Holt & Easey 1985).

South-west species

- ***Amitermes obeuntis*** (Termitidae; facultative; Fig 2) occurs throughout the south-west. Mounds are of highly variable shapes, symmetrical and domed to irregular, most commonly ≈ 20–30 cm high and wide at the base but rarely up to ≈ 50 cm high, invariably with a pitted surface, usually of dark grey colour and very high in clay content (Fig 2, Plate 2). Mounds often incorporate wood lying on the soil surface and may also be constructed against the bases of eucalypts. In such instances, they can resemble the slab-like nests of *Coptotermes acinaciformis* (Fig 1) but are generally darker in colour and lack the cracked exterior surface typical of *Coptotermes* mound/nest surfaces. Mound densities of up to 39 mounds per 0.25 ha^{-1} have been recorded for mallee-heath on granitic soils at south-coastal Fitzgerald River National Park (34° 04′ S, 119° 26′ E; Abensperg-Traun & Milewski 1995). Nests without mound structures were also located under rocks. In some places, colonies are housed below a flat shield of hard clay just below the soil surface (Fig 2). In wandoo (*Eucalyptus capillosa*) woodland of the central wheatbelt, *A. obeuntis* commonly attaches its nest to the surface of *Drepanotermes tamminensis* mounds; such nests rarely exceed 25 cm in diameter and 10 cm in depth and are readily distinguishable from the mound-proper by their darker (grey) colour. Although rare, *A. obeuntis* does occur on sandy soils that are low in clay content (heaths, some shrublands) where the species usually foregoes mound-building by attaching its nests onto the pavement mounds of *Drepanotermes rubriceps*. Mounds of *A. obeuntis* frequently provide a shelter for other termite species and at least seven species have been collected from such situations (Gay & Calaby 1970). *Amitermes obeuntis* also frequently inhabits abandoned *Drepanotermes tamminensis* mounds without attaching nests onto external mound surfaces.

- ***Coptotermes frenchi*** (Rhinotermitidae; facultative; Fig 2) occurs throughout the south-west with exception of the Swan Coastal Plain. It is locally common in eucalypt woodlands and mallee but also occurs in shrublands where emergent, mallee-type eucalypts are common. Mound-building occurs only in the eastern and south-eastern part of the species' range. Mounds are symmetrical, conical or domed, of clay, most commonly 20–30 cm high but rarely up to a maximum of ≈ 60 cm, and to 1.2 m wide at the base, with irregular networks of superficial cracks. Often mounds are built in the centre of mallee clumps (multi-stemmed eucalypts), with mallee stems protruding through the mound structure. Over 600 000 individual termites have been collected from an average-sized colony (Greaves 1967).

- ***Drepanotermes tamminensis*** (Termitidae; obligate; Fig 2) is endemic to the Western Australian wheatbelt and its distribution is restricted to the area confined by the 300 and 600 mm rainfall isohyets (Watson & Perry 1981). In the central wheatbelt, it is common on duplex soils supporting salmon gum *Eucalyptus salmonophloia*/ wheatbelt wandoo *E. capillosa* woodland and in shrublands on gravelly soils where mound densities may be particularly high (Park *et al.* 1994; M Abensperg-Traun, unpublished data). Park *et al.* (1994) give average numbers of termite individuals within single mounds of

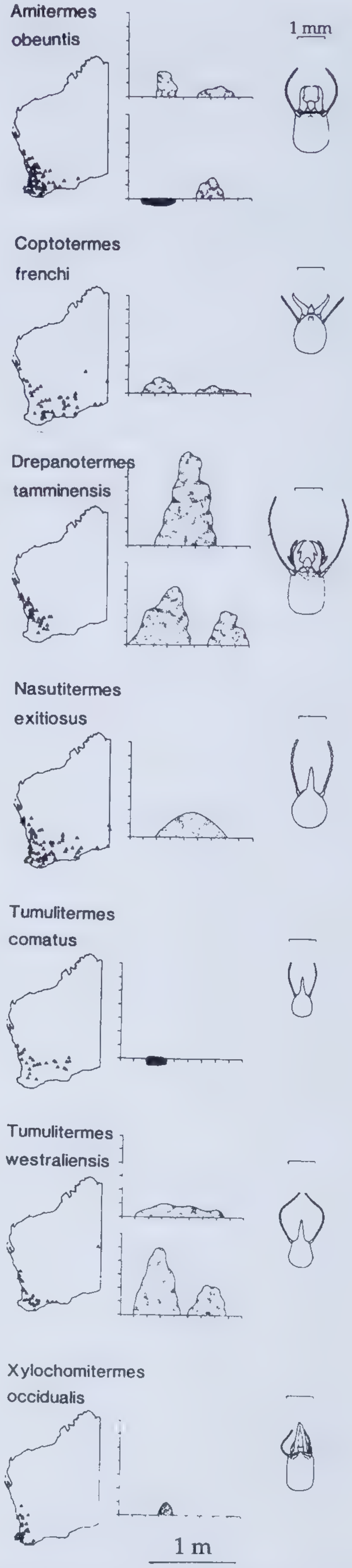
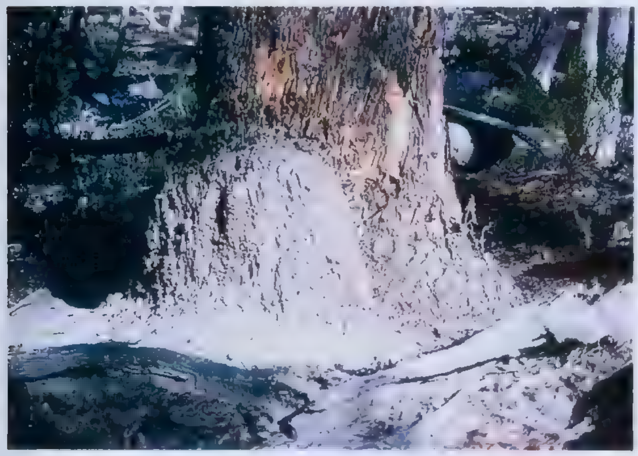
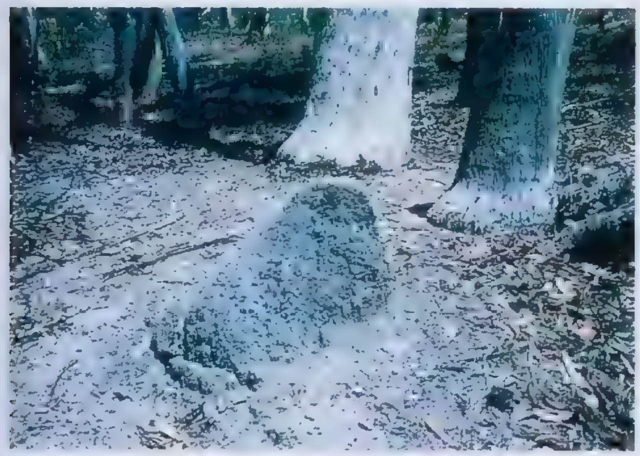
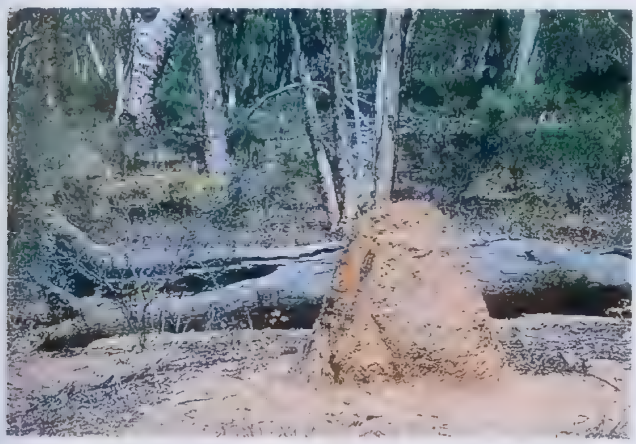
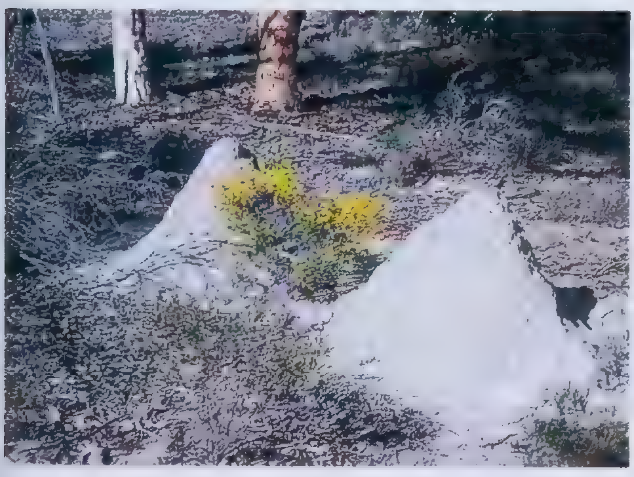


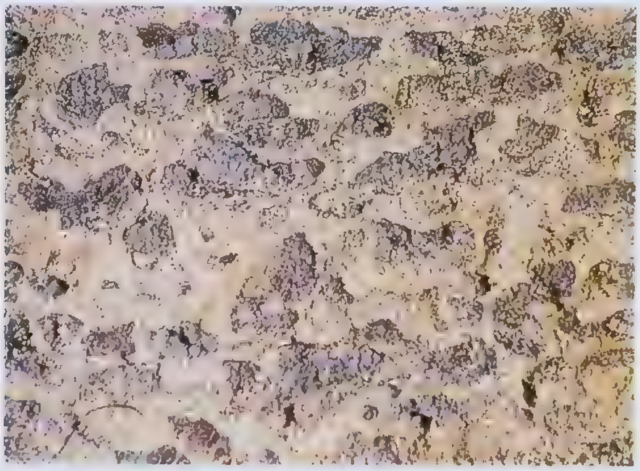
Figure 2. Western Australian mound-building termite species that are restricted to all or parts of the south-west, common mound shapes and dimensions, and a dorsal view (and dimension) of soldier head-capsules for respective species.











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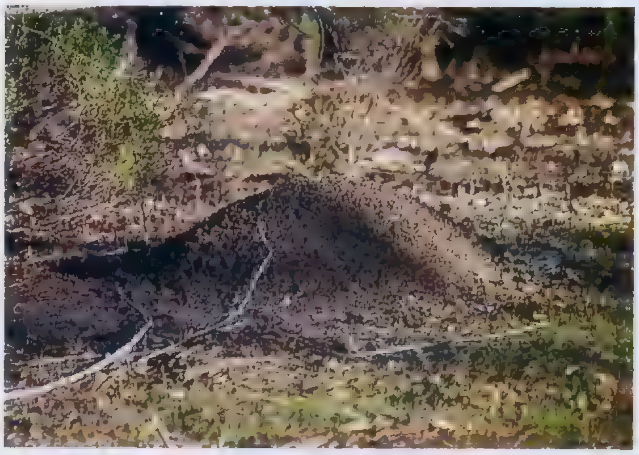

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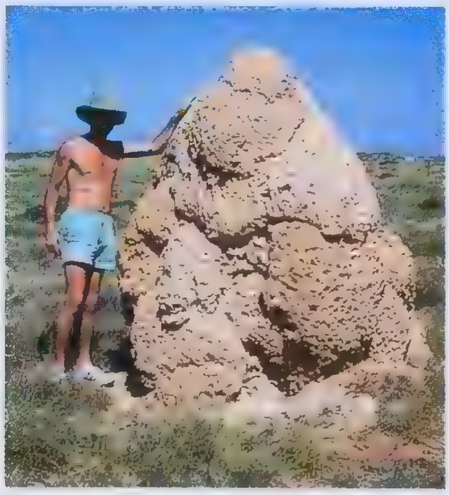

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Plate 1. 'Lean-to' slab nest of *Coptotermes acinaciformis* (wandoo *Eucalyptus capillosa* woodland, Kellerberrin, central wheatbelt).

Plate 2. Mound of *Amitermes obeuntis* (wandoo *Eucalyptus capillosa* woodland, Kellerberrin, central wheatbelt).

Plate 3. Mound of *Drepanotermes tamminensis* (wandoo *Eucalyptus capillosa* woodland, Kellerberrin, central wheatbelt).

Plate 4. Mounds of *Drepanotermes tamminensis* (wandoo *Eucalyptus capillosa* woodland, Kellerberrin, central wheatbelt).

Plate 5. Characteristic surface of *Drepanotermes tamminensis* mound (Kellerberrin, central wheatbelt).

Plate 6. *Nasutitermes exitiosus* mound (wandoo *Eucalyptus capillosa* woodland, Kellerberrin, central wheatbelt).

Plate 7. *Nasutitermes triodiae* mound (spinifex *Triodia* spp. grassland, Exmouth).

29 000 (wandoo woodland) and 22 000 (shrubland on gravelly soils). This suggests differences in habitat suitability between these two vegetation types. The species is largely absent from gimlet *Eucalyptus salubris* woodland (on heavier soils in lower-lying areas), mallee, york gum *E. loxophleba*/jam *Acacia acuminata* woodland and from vegetation on deep sands where the pavement mounds of *D. rubriceps* may be common (see above; M Abensperg-Traun, personal observations). Mounds are a mixture of sand and clay, irregularly conical or rounded, 0.5–1.5 m high and wide at the base (Plate 3). As is the case for most species, their mounds may vary markedly in colour depending on soil type (Plate 4). The aggregated nature of mounds suggests that, as is the case for *D. perniger* and possibly other species of mound-building *Drepanotermes*, individual colonies may construct several mounds to house the growing colony. With the exception of young mounds, mound-surfaces are characteristically 'spotty', with dark patches of approximately 2–3 cm in diameter covering varying proportions of the mound surface (Plate 5). These represent chambers eroded by wind and rain where termite workers deposit waste material such as feces and dead termites. Mound extensions cover eroded chambers with a new surface which is usually creamy-grey in color but depending on soil type. In old and/or senescent colonies, eroded chambers may cover a high proportion of the mound surface.

- ***Nasutitermes exitiosus*** (Termitidae; facultative; Fig 2) occurs throughout the south-west and is common in eucalypt forests, eucalypt woodlands and mallee. In the Fitzgerald River National Park along the south-coast, it also occurs in shrublands where emergent ('mallee-form') eucalypts are common. In the central wheatbelt it is rare or absent from sandy soils (mixed shrublands, heath) and from shallow soils supporting york gum *E. loxophleba*/jam *Acacia acuminata* woodlands. Mounds are usually symmetrical, dome-shaped and smooth (Plate 6). The species requires no clay for mound-building, constructing soft exterior mound walls of earthy material ≈ 2-4 cm thick, protecting a hard, blackish carton nest core (composed of fecal material). Mounds are generally ≈ 20–30 cm high and wide, but may reach ≈ 70 cm in height and width in higher rainfall regions. Large mounds frequently have steeper sides than is shown in Fig 2 and may then become somewhat less symmetrical. Mounds become progressively smaller with decreasing rainfall (and increasing temperature extremes) where nests may be entirely below ground level. Where the colony has died, the earthy mound cover is progressively eroded, exposing the dark and brittle carton nest core. In areas of heavy rocky outcropping where soil is scarce, mounds may lack the outer layer of soil. Gay & Whetherly (1970) collected more than 2.5 million individuals from a single large mound. In contrast to the mounds of most other species, no other termite species has been found to co-inhabit mounds of *N. exitiosus* until the death of the mound builder.

- ***Tumulitermes comatus*** (Termitidae; facultative; Fig 2) occurs throughout most of the south-west. Mound-building is largely restricted to coastal areas such as the heath/shrublands between Yanchep (31° 33′ S, 115° 41′ E) and Dongara (29° 15′ S, 114° 56′ E). The sand and clay mounds may protrude slightly above the soil surface but are generally level with the soil surface and to ≈ 25 cm wide.

- ***Tumulitermes westraliensis*** (Termitidae; obligate; Fig 2) is endemic to Western Australia with its distribution broadly defined by the 400 mm rainfall isohyet. A single (questionable?) record locates the species at the Giles Meteorological Station in the Simpson Desert (25° 02′ S, 128° 18′ E; Watson & Abbey 1993). The species is also common on the sandy Swan Coastal Plain and on the Darling Range (Ratcliffe *et al.* 1952). Mounds are of sand and clay and of two principal shapes; wide and flat (pavement-like) and ≈ 10–30 cm high (south-coastal) (and thus resembles some of the mounds of *Drepanotermes rubriceps* and *D. perniger*), or up to ≈ 100 cm high and broadly conical in northern parts. In Fitzgerald River National Park, up to 31 mounds per 0.25 ha^{-1} have been recorded for mallee-heath on granitic soils. Here, only pavement-like mounds were built and the species was absent from heath (on sands), and from coastal marlock *Eucalyptus platypus* and flat-topped yate *E. occidentalis* woodlands (Abensperg-Traun & Milewski 1995).

- ***Xylochomitermes occidualis*** (Termitidae; facultative; Fig 2) occurs throughout the forested regions of the south-west, extending into the central wheatbelt near Kellerberrin (not shown by distributional data of Watson & Abbey 1992). The mounds are usually blackish or brownish, of carton and soil, symmetrical, domed and ≈ 10–15 cm high and wide. Mound-building has been observed in southern eucalypt forests of the extreme south-west (Perry *et al.* 1985), and near Mundaring Weir east of Perth (31° 58′ S, 116° 10′ E), but not elsewhere in the region.

Arid centre species

- ***Drepanotermes columellaris*** (Termitidae; facultative; Fig 3) is endemic to Western Australia where its habitats are dominated by mulga (*Acacia aneura*) woodland/shrubland. The sand and clay mounds of "northern" populations are pillar-like structures 1–2 m high and 0.5–1 m wide at the base and cylindrical or tapered to the top. Some mounds fork in upper parts, forming two or more turrets up to 0.5 m long. Mounds are often situated under tall vegetation. Southern populations rarely build mounds (Watson & Perry 1981).

- ***Microcerotermes boreus*** (Termitidae; facultative; Fig 3) is found in the predominantly arid western half of the State extending south of the Tropic of Capricorn to an area approximately level with Lake Moore north-east of Dalwallinu (30° 17′ S, 116° 40′ E). An apparently isolated population has been recorded for a small area in the tropical Kimberley region near the Mitchell Plateau (14° 44′ S, 125° 44′ E). Mound-building has been observed only in tropical areas of its Western Australian distribution where it constructs small, rounded, blackish carton-nests approximately 25 cm high and wide at the base (Gay & Calaby 1970).

- ***Tumulitermes tumuli*** (Termitidae; facultative; Fig 3) is predominantly a species of the mulga lands of the arid interior although south-western populations extend into the agricultural region as far south as Moora (30° 39′ S, 116° 00′ E). Mounds are made of sand and clay, broadly symmetrical, spire-like and to ≈ 60–70 cm high, with a

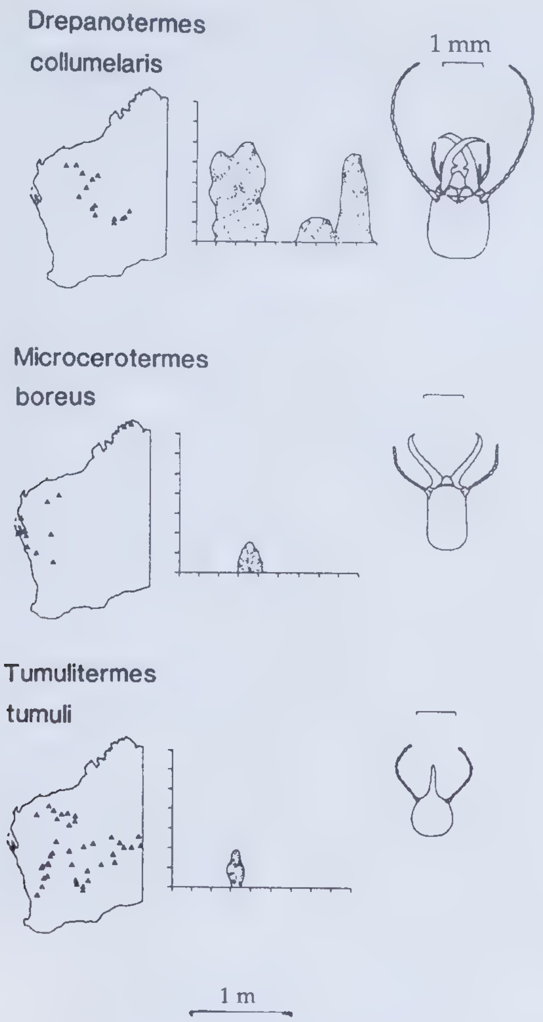

Figure 3. Western Australian mound-building termite species that are largely restricted to the central arid region, common mound shapes and dimensions, and a dorsal view (and dimension) of soldier head-capsules for respective species.

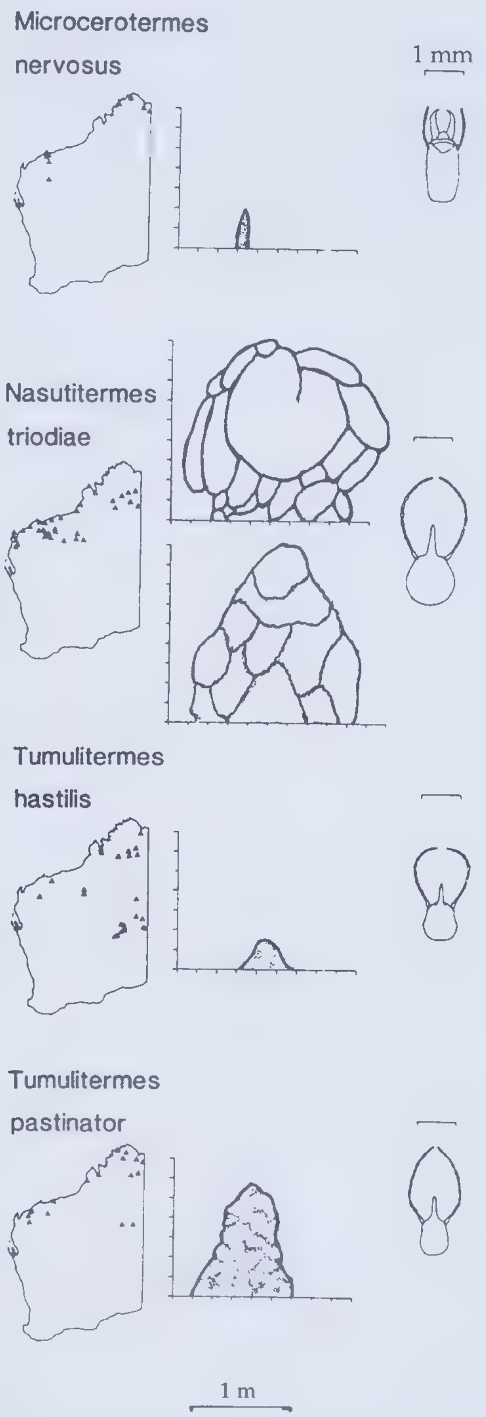

Figure 4. Western Australian mound-building termite species that are largely restricted to the area north of the Tropic of Capricorn, common mound shapes and dimensions, and a dorsal view (and dimension) of soldier head-capsules for respective species.

pronounced constriction at the base where it is ≈ 15–20 cm wide. Sheep frequently rub against mounds which readily snap off at the base, but these are commonly rebuilt by the colony.

Northern species

- ***Microcerotermes nervosus*** (Termitidae; facultative; Fig 4) builds small, pointed mounds, composed of predominantly dense woody carton with a thin outer layer of soil particles, in northern parts of their range (Kimberley). Mounds are frequently constructed over dead stumps or against the base of a tree (Gay & Calaby 1970). Mound-building has not been observed in more southerly populations.

- ***Nasutitermes triodiae*** (Termitidae; obligate; Fig 4, mound in upper position redrawn from Ratcliffe *et al.* 1952) is predominantly a species of spinifex (hummock) grasslands (*Triodia* spp). Its sand and clay mounds are the largest of any species in Western Australia (to ≈ 4 m high). Mounds are of variable shapes with rounded or pointed tops, dome- or mushroom-shaped, and are often constricted at the base. Mounds may be smooth or covered in bulbous lobes, each lobe representing an individual (nocturnal) mound extension effort (Plate 7).

- ***Tumulitermes hastilis*** (Termitidae; obligate; Fig 4) inhabits predominantly mixed scrub/ grasslands. The sand and clay mounds are up to ≈ 40 cm high and wide at the base. Mounds may reach high local densities.

- ***Tumulitermes pastinator*** (Termitidae; obligate; Fig 4) occurs in grass/scrubland and is particularly common on the poorest soils, sandy gravel to stony country (Gay & Calaby 1970). Mounds are of sand and clay, broadly conical and commonly ≈ 60–80 cm high and wide but can reach a maximum height of ≈ 2 m. Individual colonies may construct several mounds which are termed polycalic (Holt & Easey 1985).

Coastal or near-coastal species

• ***Coptotermes brunneus*** (Termitidae; obligate; Fig 5) is restricted to a near-coastal strip north of the Murchinson River inhabiting sclerophyll woodland and mallee scrub. Its distribution closely matches that of its obligate inquiline (co-inhabitant) *Ahamitermes inclusus* (see below). Mounds are symmetrical, conical or domed, of clay and to a maximum of ≈ 2.5 m high and 1.5 m wide at the base. In mature mounds (>≈ 1.5 m high), the mound interior may almost entirely be a mass of clay, with most of the actual nest below ground level; the mound interior may also be cavernous (Calaby & Gay 1956; Calaby & Gay 1959). Gay & Calaby (1970) report that the upper portion of the mound interior may contain small pools of free water. One of us (DHP) found internal walls of some very large, old mounds to be lined with elongate "collecting cups" of clay, 2–3 cm wide and 10–20 cm long, holding small amounts of water that has condensed off the inside walls.

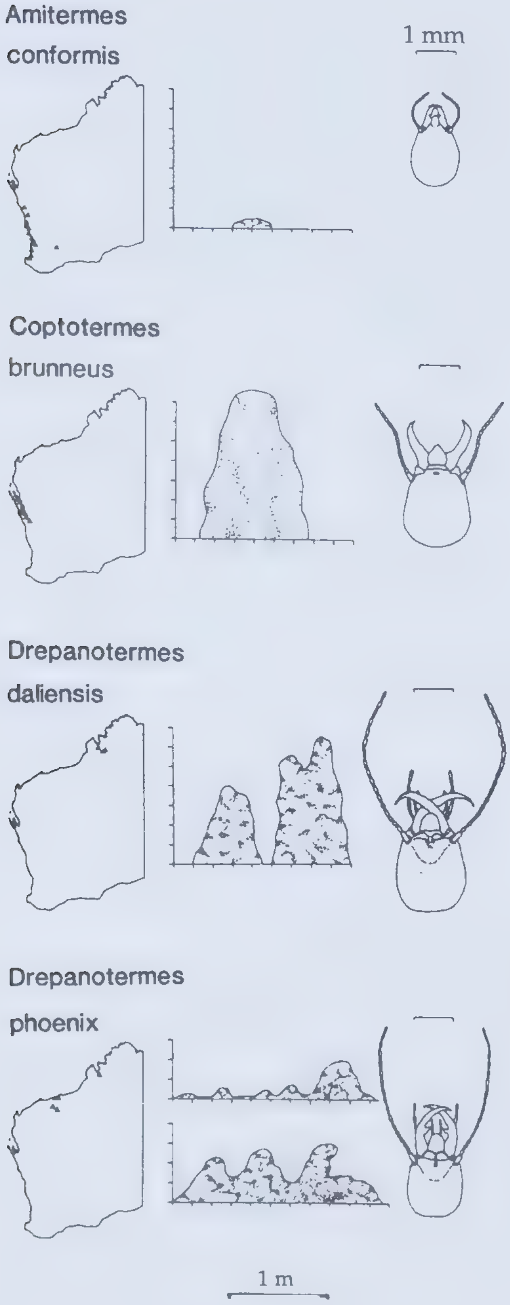

Figure 5. Western Australian mound-building termite species that are restricted to coastal or near-coastal regions, common mound shapes and dimensions, and a dorsal view (and dimension) of soldier head-capsules for respective species.

• ***Amitermes conformis*** (Termitidae; facultative; Fig 5) is restricted to a coastal strip from approximately Busselton in the south (33° 39′ S, 115° 20′ E) to just north of Kalbarri (27° 43′ S, 114° 10′ E). A single record also places the species in the southern wheatbelt south of Merredin (31° 29′ S, 118° 17′ E). Mounds are found only in eucalypt woodland and forest in southern-most areas of its distribution and are of sand and clay, 5 – 10 cm high and ≈ 20 cm wide at the base.

• ***Drepanotermes daliensis*** (Termitidae; facultative; Fig 5) shows a very restricted distribution around the coastal town of Broome (17° 58′ S, 122° 14′ E). Mounds (of sand and clay) are columnar to 1.5 m high, or broadly conical and rounded, 0.5–1 m high and wide at the base. Mounds may have more than one turret, similar to the mounds built by *D. columellaris* (Watson & Perry 1981).

• ***Drepanotermes phoenix*** (Termitidae; obligate; Fig 5) is endemic to Western Australia and inhabits a restricted area of predominantly spinifex grasslands near the coastal town of Roebourne (20° 47′ S, 117° 09′ E). Mounds are of sand and clay, pavement-like and 1–3 m in diameter from which rise a series of irregular hummocks up to ≈ 80 cm in height (Watson & Perry 1981).

Kimberley species

Tropical regions are known for the large size and abundance of its termite mounds (*e.g.* Andersen & Jacklyn 1993), and in the tropical Kakadu National Park of the Northern Territory, 16 species (about 30% of all known species in the region) build mounds (Braithwaite *et al.* 1988). This compares with six species (8%) for the termite fauna in the Western Australian wheatbelt. We therefore expect that the incidence of mound-building in the tropical Kimberley of Western Australia, for which our observations are least comprehensive, will increase as more data become available. For example, five other (termitid) species whose distributions overlap that of the Kimberley region are known to build mounds in the adjacent northern tropics of the Northern Territory (Braithwaite *et al.* 1988), and may therefore also build mounds in the Kimberley region. These species include *Amitermes vitiosus*, *Macrognathotermes sunteri*, *Microcerotermes nanus*, *M. serratus* and *Xylochomitermes melvillensis* (Table 1). Of these, *Macrognathotermes sunteri*, *Microcerotermes nanus* and *Xylochomitermes melvillensis* are largely restricted to the Kimberley region of their Western Australian distribution (Watson & Abbey 1993).

Identification of the original mound builder

As the above observations indicate, the presence of a termite species within a mound does not necessarily imply its role as the mound-builder. Not only are mounds sometimes taken over by other termite species, but mounds are commonly inhabited simultaneously by several species although without sharing galleries and chambers.

Subterranean (non-mound-building) termite species living in the mounds of other (mound-building) termites are referred to as 'inquilines'. This behaviour is common; it has been observed in a wide range of species and inquilines may occur in the presence or absence of the colony of the original mound builder. Old colonies, or those weakened by disease, predation (*e.g.* ants, echidnas) or low food availability, are likely to be more susceptible to invasion by inquilines (or predaceous ants) than healthy colonies. Low food availability may occur during drought (especially through competition with livestock for grass, Watson & Gay 1970) or following fire (*e.g.* Abensperg-Traun *et al.* 1996). Benefits to the inquiline may include greater protection from environmental fluctuations (temperature and moisture extremes) afforded by mound-walls, possibly reduced predation by ants, the obvious reduction of energy expenditure involved in mound construction and maintenance, and being able to feed on nest content, especially in nests that contain carton (faecal) material. Several wood-eaters such as *Macrognathotermes sunteri* are known to feed on carton material from *Coptotermes* mounds (Miller 1991). Other species may invade mounds of grass-eaters for the food stores that they contain. All three species of the Australian endemic *Ahamitermes* (*A. hillii, A. nidicola, A. inclusus*) are obligate inquilines in the nests of *Coptotermes* spp (Calaby 1956). Of these, *A. hillii* and *A. inclusus* are endemic to Western Australia. The distribution of *Ahamitermes hillii* matches that of *Amitermes obeuntis* (Fig 2), while that of *Ahamitermes inclusus* closely resembles that of its host *Coptotermes brunneus* (Fig 5, Watson & Abbey 1993). Most other inquilines are opportunistic (facultative) mound inhabitants. For north-east Queensland, Spain & Brown (1979) report up to 81 % and 52 % of *Amitermes laurensis* and *A. vitiosus* mounds, respectively, housing one or more inquiline. We have made similar observations for Western Australian species involving subterranean opportunists as well as mound-builders inhabiting the mounds of other species (*e.g.* some *Drepanotermes* spp). In the central wheatbelt, subterranean opportunists frequently found in the mounds of *Drepanotermes tamminensis* include *Heterotermes occiduus, Microcerotermes newmani, Tumulitermes petilus, T. peracutus, Amitermes neogermanus* and several species of the *Termes-Capritermes* complex such as *Ephelotermes argutus* and *Xylochomitermes occidualis* (M Abensperg-Traun, unpublished data). *Amitermes obeuntis* is a mound-builder that commonly inhabits *D. tamminensis* mounds.

The presence of inquilines may make it difficult to correctly identify the original mound builder. Structural integrity of mounds, which can generally be used as a rough indicator of colony vigour, is maintained through mound extension to accommodate the growing colony. Mounds housing healthy colonies rarely show extensive invasions by other termite species. However, following the decline of the original colony, mound expansion is likely to cease. The mound then falls into increasing disrepair and structural degradation which is generally reflected by a crumbly outer surface covered to varying degrees by lichen, and usually by extensive ant invasion (*e.g. Iridomyrmex greensleidi* and *I. rufoniger* in the central wheatbelt). Such mounds frequently house several species of termites (and ants) which may occupy the bulk of the mound interior.

Correct identification of the original mound builder involves identification of the species occupying most of the mound interior, as well as those of other mounds in the close vicinity, and by comparing physical mound characteristics with those given in this review (with regard for geographic location). Entry into the mound to collect specimens for later identification may require a pick-axe, crow-bar and/or spade. Using forceps and taking great care to avoid damage to specimens, a minimum of ten soldiers and workers each should be collected for species identification from each individual mound, and from all co-inhabiting species. Specimens should be immediately stored in vials containing ≈ 75% alcohol for subsequent identification. Each individual collection (soldiers and workers of one species) must be stored in separate vials, labelled for location and any other relevant detail (*e.g.* longitude/latitude, mound shape and dimensions, vegetation and soil type). For more detailed taxonomy, see Hill (1942), Watson & Perry (1981), Perry *et al.* (1985) and Miller (1991).

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Morphological and genetic discrimination of new species and subspecies of gekkonid and scincid lizards (Squamata: Lacertilia) from the Carnarvon Basin region of Western Australia

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Abstract

Two new species and one new subspecies of lizards are described under the gekkonid genus *Diplodactylus* and the scincid genera *Ctenotus* and *Menetia*. The gecko *Diplodactylus klugei* sp nov and the skink *Ctenotus maryani* sp nov both qualify as 'cryptic species' in the sense that they are morphologically similar but genetically distinct from sympatric congeners. The skink *Menetia surda cresswelli* subsp nov is morphologically distinct from the typical race but shows only a minimal level of genetic divergence in allopatry. The three taxa clearly illustrate the frequent lack of congruence between morphological and genetic differentiation among squamates. A plea is made for more routine use of allozyme analysis to detect 'cryptic' species within regional vertebrate faunas.

Introduction

The Carnarvon Basin region of northwest Western Australia is an area of exceptional reptile diversity with more than 120 species recorded as a consequence of herpetological surveys conducted during the mid 1970s to early 1980s (Storr & Hanlon 1980; Storr & Harold 1978, 1980, 1984; Storr *et al.* 1983). In 1995–97 the area was resampled as part of the southern Carnarvon Basin Biological Survey, a joint project of the Western Australian Department of Conservation and Land Management and the Western Australian Museum. Close study of the combined regional collections, now totalling over 11000 specimens, has led to the recognition of new species within the genera *Ramphotyphlops* (Typhlopidae), *Crenadactylus* and *Diplodactylus* (Gekkonidae), *Delma* (Pygopodidae), and *Ctenotus, Cryptoblepharus, Lerista* and *Menetia* (Scincidae). In most cases, clarification of formal taxonomy will require large scale revisionary studies, several of which are currently in progress. However, in a few cases the taxonomic issues were largely confined to the Carnarvon Basin or adjacent regions and thus could be resolved without major revisionary work.

In this paper we describe two new species and one new subspecies of lizards belonging to the genera *Diplodactylus, Ctenotus* and *Menetia* respectively. Allozyme electrophoresis has been used to demonstrate reproductive isolation between sympatric congenors and/or to determine the level of genetic differentiation between allopatric populations.

Materials and Methods

Species detection and morphometric analysis

The new taxa were initially detected by careful examination of voucher specimens obtained from the Biological Survey sampling quadrats (each with an area of 16 ha). In the case of the new *Ctenotus* and *Diplodactylus* species, material provisionally identified as *C. iapetus* Storr and *D. pulcher* (Steindachner) showed subtle but consistent patterns of variation which led to suspicions that the samples might each contain more than one biological species. Material of each potential species-composite was initially divided up according to quadrat and sex. Starting with one of the more peripheral localities (*e.g.* most easterly), the material of each sex was examined in turn, paying close attention to the nature of any variation within and between each quadrat sample. By working systematically through the voucher material in this way, it was possible to detect subtle but systematic shifts in character states which might otherwise be overlooked as intrapopulational variation. Each of "*C. iapetus*" and "*D. pulcher*" were divided into two putative species.

Allozyme electrophoresis was then used to test for the presence of more than one biological species in each case. The 'null hypothesis', that all of the individuals are drawn from a single, freely interbreeding population, would be supported by random allelic variation between the two putative taxa. Rejection of the null hypothesis (*i.e.* recognition of discrete, reproductively isolated populations) would be indicated where significant non-random patterns of allelic variation are observed. In the case of sympatric populations, a lack of interbreeding constitutes strong grounds for recognition of distinct species, irrespective of which of the various contemporary species concepts is followed (see Baum (1992) for an introduction to this literature; and Frost & Hillis (1990) for some herptological examples).

Once the existence of an additional taxon was confirmed by allozyme electrophoresis, all available voucher specimens from the wider study area were examined. This phase of the analysis allowed for a wider assessment of the degree of congruence among the various 'diagnostic' morphological features and provided an indication of the wider distribution of each taxon.

In the case of *Menetia surda*, the majority of Carnarvon Basin specimens conformed to a single 'morph', but this differed from 'typical' *M. surda* from the northwest of Western Australia. Specimens from a geographically intermediate population on Mardathuna appeared morphologically distinct from both northwestern and southern populations. In this case, allozyme electrophoresis was used to estimate the level of genetic differentiation between the various allopatric (and thus, by definition, reproductively isolated) populations.

The following measurements were taken with vernier calipers for all taxa: SVL (snout-vent length); Tail (tail length); and ForelimbL (length of forelimb including manus). The hindlimb was measured as HindlimbL (length of hindlimb including pes) for skinks but as TibialL (length of lower hindlimb, from upper surface of knee to plantar surface of pes) and BifemoralW (combined upper hindlimb width, measured across the knees with femora in horizontal plane) for *Diplodactylus*; this reflects differences in the most frequent preservational posture, namely hindlimbs extended in the skinks but flexed in the gekkos. Two measurments were taken of the head in *Diplodactylus*, namely; HeadL (measured from tip of snout to anterior margin of auricular fossa); and HeadW (maximum width of head).

Except where noted, head scale terminology follows Taylor (1935) for skinks and Kluge (1967) for *Diplodactylus*. Paravertebral scales (PV) in skinks were counted from immediately behind the parietal scales down to a point opposite the vent. Subdigital lamellae (SDL) were counted on the longest finger (3rd; SDLM3) and longest toe (4th; SDLP4), from the point of divergence of the digit up to, but not including, the claw-sheath. For purposes of pattern description of skinks, longitudinal scale rows are numbered outward from the paravertebral series (SR-1) around to the ventral midline (*e.g.* SR-13). Midbody scales rows (MBS) were counted midway between the axilla and groin in skinks.

Statistical analyses of individual measurements and scale counts were performed by analysis of variance. Before performing interspecific analyses, each sample was examined for intraspecific sexual dimorphism. In all cases, this was found to be non-significant (*i.e.* $P > 0.05$) for the measured variables. Relative limb lengths were examined by ratios calculated against SVL; these values are not directly amenable to statistical analysis (Atchley *et al.* 1976) but provide a useful guide to interspecific differences in shape.

Unless otherwise indicated, specimen registration numbers refer to the herpetological collection of the Western Australian Museum. The sex of voucher specimens was determined by dissection and inspection of gonads.

Allozyme electrophoresis

Liver samples suitable for allozyme electrophoresis were removed from freshly-killed lizards in the field or at the WA Museum. Samples were frozen in liquid nitrogen immediately after removal and stored at -80 °C.

Allozyme electrophoresis of liver homogenates was conducted on cellulose acetate gels ('Cellogel', MALTA) according to the methods of Richardson *et al.* (1986). The following enzymes or non-enzymatic proteins exhibited zygograms of sufficient activity to proceed for at least one species-group: aconitate hydratase (*Acon*, EC 4.2.1.3), acid phosphotase (ACP, EC 3.1.3.2), aminoacyclase (*Acyc*, EC 3.5.1.14), alcohol dehydrogenase (*Adh*, EC 1.1.1.1), adenlyate kinase (*Ak*, EC 2.7.4.3), albumin (*Alb*), carbonate dehydratase (*Ca*, EC 4.2.1.1), diaphorase (*Dia*, EC 1.6.99), enolase (*Enol*, EC 4.2.1.11), esterase (*Esi*, EC 3.1.1.?), fructose-bisphosphatase (*Fdp*, EC 3.1.3.11), fumarate hydratase (*Fum*, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (*Gapd*, EC 1.2.1.12), guanine deaminase (*Gda*, EC 3.5.4.3), glutamate dehydrogenase (*Gdh*, EC 1.4.1.13), lactoyl-glutathione lyase (*Glo*, EC 4.4.1.5), aspartate aminotransferase (*Got*, EC 2.6.1.1), glucose-6-phosphate dehydrogenase (*G6pd*, EC 1.1.1.49), glycerol-3-phosphate dehydrogenase (*Gpd*, EC 1.1.1.8), glucose-6-phosphate isomerase (*Gpi*, EC 5.3.1.9), alanine aminotransferase (*Gpt*, EC 2.6.1.2), glutathione peroxidase (*Gpx*, EC 1.11.1.9), glutathione reductase (*Gsr*, EC 1.6.4.2), 3-hydoxybutyrate dehydrogenase (*Hbdh*, EC 1.1.1.30), isocitrate dehydrogenase (*Idh*, EC 1.1.1.42), cytosol aminopeptidase (*Lap*, EC 3.4.11.1), L-lactate dehydrogenase (*Ldh*, EC 1.1.1.27), malate dehydrogenase (*Mdh*, EC 1.1.1.37), 'malic' enzyme (*Me*, EC 1.1.1.40), mannose-6-phosphate isomerase (*Mpi*, EC 5.3.1.8), nucleoside-diphosphate kinase (*Ndpk*, EC 2.7.4.6), purine-nucleoside phosphorylase (*Np*, EC 2.4.2.1), dipeptidase (*PepA*, EC 3.4.13), tripeptide aminopeptidase (*PepB*, EC 3.4.11), proline dipeptidase (*PepD*, EC 3.4.13), phosphoglycerate mutase (*Pgam*, EC 5.2.4.1), phosphogluconate dehydrogenase (*6pgd*, EC 1.1.1.44), phosphoglycerate kinase (*Pgk*, EC 2.7.2.3), phosphoglucomutase (*Pgm*, EC 5.4.2.2), pyruvate kinase (*Pk*, EC 2.7.1.40), superoxide dismutase (*Sod*, EC 1.15.1.1), L-iditol dehydrogenase (*Sordh*, EC 1.1.1.14), and triose-phosphate isomerase (*Tpi*, EC 5.3.1.1). The nomenclature for identifying loci and allozymes is outlined by Adams *et al.* (1987).

Genetic distances were expressed as percentage fixed differences (% FD, Richardson *et al.* 1986) and Nei's unbiased genetic distance (Nei D; Nei 1978). Heterozygosity values for each taxon were calculated as the proportion of all genotypes observed to be heterozygotes, averaged over all loci.

Systematics

Family Gekkonidae

Diplodactylus klugei sp nov

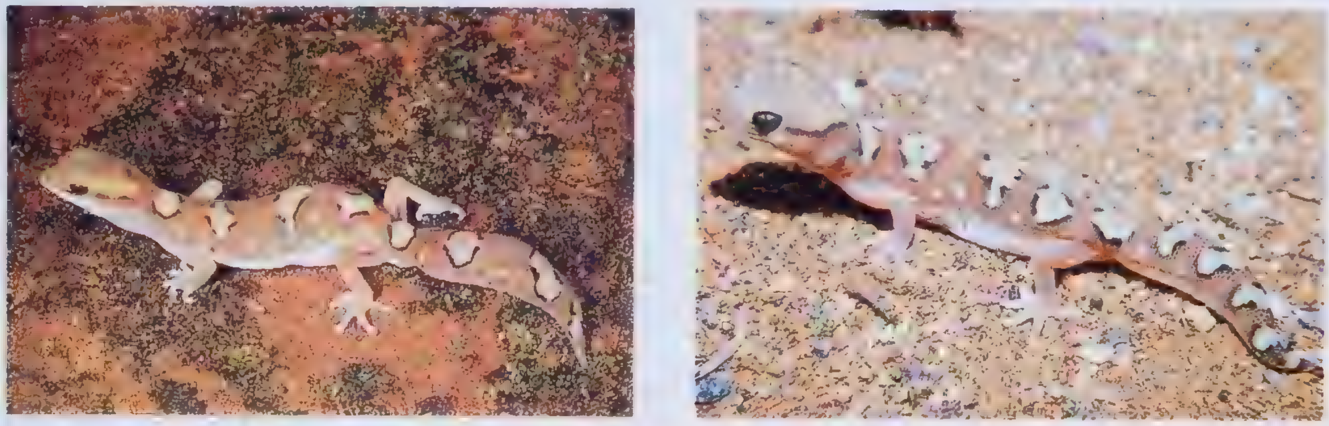
(Fig 1A)

Holotype

R120941 in the collection of the Western Australian Museum, an adult female collected on 11/10/1994 at Biological Survey quadrat WO4, 7 km SE of Woodleigh Outstation in 26° 11′ 30″ S, 114° 30′ 34″ E (Fig 2).

Paratypes (Biological Survey quadrats in boldtype)

14 km W Giralia HS (2-2° 40′ S, 114° 14′ E): 61089; 26



A. *Diplodactylus klugei*

B. *Diplodactylus pulcher*

Figure 1. Individuals of *Diplodactylus klugei* sp nov. and *D. pulcher* (Steindachner), illustrating the close similarity of these probable sibling species. Details of specimens as follows; *D. klugei*, WAM R131016, an adult male from 11 km WNW Woodleigh Outstation, photographed by B Maryan; *D. pulcher*, an adult female from Kambalda East, photographed by B Maryan. Note the relatively larger head and eye of *D. pulcher*.

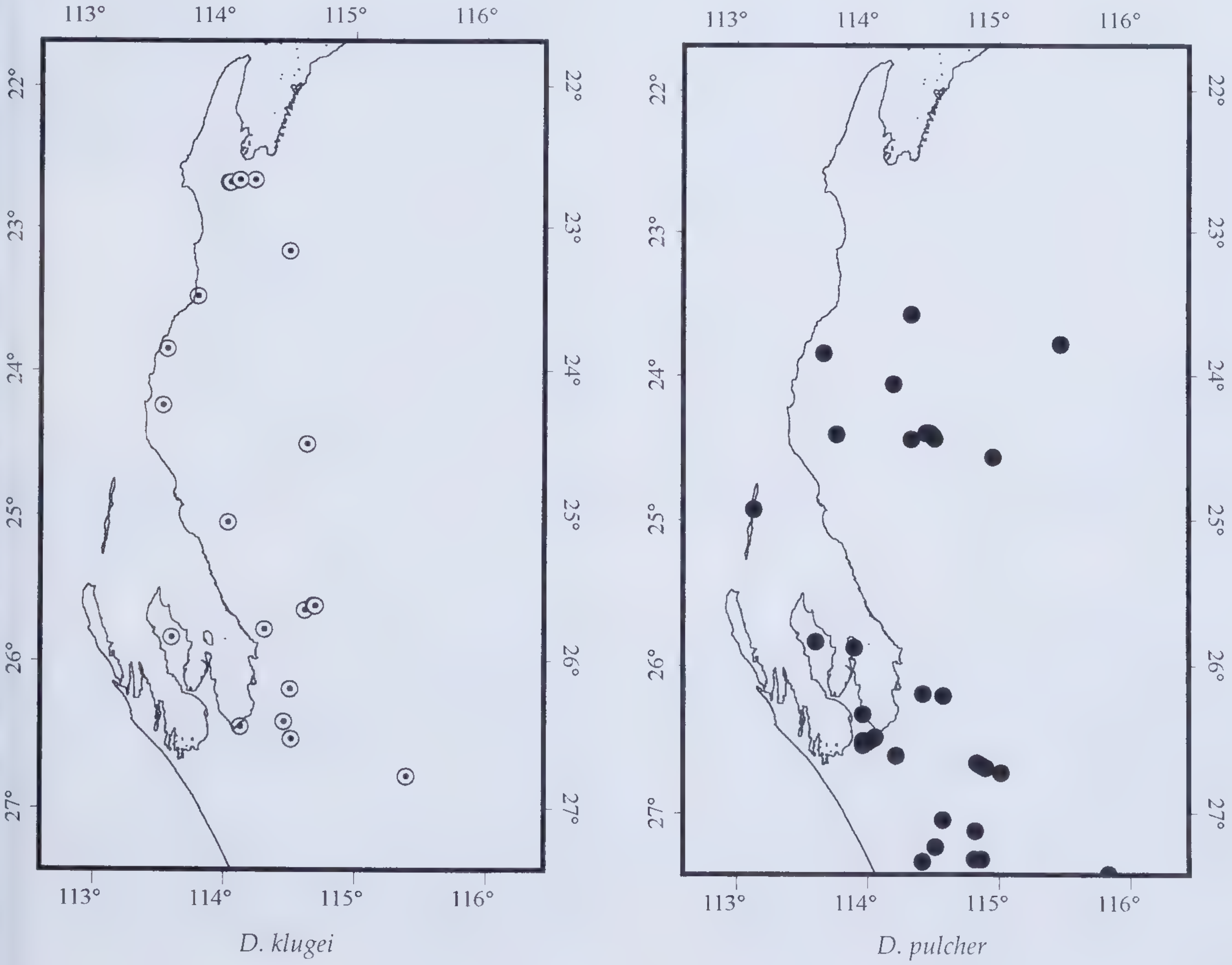


Figure 2. Distribution of *Diplodactylus klugei* sp nov and *D. pulcher* in the Carnarvon Basin area of Western Australia where they occur in regional sympatry. *Diplodactylus pulcher* is widely distributed outside of the study area.

km W Giralia HS (22° 40′ S, 114° 07′ E): 61265-66; Bullara (22° 41′ S, 114° 02′ E): 60412-13; 2 km E Bullara HS (22° 41′ S, 114° 03′ E): 61129-32; 3 km W Winning HS (23° 10′ S, 114° 30′ E): 71308; Warroora (23° 29′ S, 113° 48′ E): 8159-60; 5 km SE Gnaraloo HS (23° 51′ S, 113° 34′ E): 71572; **CU1**, 14 km E Cape Cuvier (24° 14′ 41″ S, 113° 32′ 07″ E): 126905; **MR1**, 9.8 km E Mardathuna HS (24° 30′ 41″ S, 114° 38′ 13″ E): 120715, 123460, 126758; Callagiddy HS (25° 03′ S, 114° 02′ E): 36748, 40669, 41589; **MD2**, 9.7 km NE Meedo HS (25° 37′ 23″ S, 114° 41′ 39″ E): 120982, 121013, 122579, 122658, 122666, 124989; **MD1**, 10.9 km NE Meedo HS (25° 37′ 31″ S, 114° 42′ 16″ E): 121050, 122527, 122550-51, 122560, 122650, 126691; **MD3**, 1.25 km NE Meedo HS (25° 39′ 14″ S, 114° 37′ 33″ E): 121610; 18.4 km N Yaringa HS (25° 47′ S, 114° 19′ E): 71110; 11 km WNW Woodleigh OS (26° 09′ S, 114° 26′ E): 131016; **WO4**, 7 km SE Woodleigh OS (26° 11′ 30″ S, 114° 30′ 34″ E): 120872, 120884, 120925, 120939, 122961, 125075; **WO5**, 13.5 km SE Woodleigh OS (26° 11′ 44″ S, 114° 25′ 24″ E): 120870, 120881; Overlander Roadhouse (26° 25′ S, 114° 28′ E): 15278, 55189; 7 km W Hamelin HS (26° 27′ S, 114° 08′ E): 54843; 10 M S Shark Bay turnoff, Northwestern Highway (26° 32′ S, 114° 31′ E): 28654; 6 km NE Mungawolagudi (26° 47′ S, 115° 24′ E): 60618.

Diagnosis

A moderate-sized member of subgenus *Diplodactylus* with rostral and first supralabial both entering nostril; posterior supralabials not much larger than general head scales; mental in long contact with first infralabial; digits with single pair of enlarged apical plates, claws project well forward of plates; other subdigital scales small, rounded, arranged in transverse rows; dorsal pattern usually a series of 4-5 large, dark-rimmed pale blotches on red-brown ground colour (blotches are occasionally united into broad, dark-edged vertebral stripe).

Description

A slender-bodied, moderately long-limbed terrestrial *Diplodactylus*. Tail shorter than head + body, round in cross-section, widening slightly from base and tapering gradually to tip. Head relatively long and narrow, with distinctly 'beaked' snout. SVL to 58 mm; Tail to 33 mm; HeadL to 11.1 mm; HeadW to 9.0 mm; TibialL to 9.0 mm; BifemoralW to 20.5 mm. Other statistical data are given in Table 1. Males have higher mean values than females for every dimension but none of the contrasts is statistically significant.

General head and body scalation finely granular, granules slightly larger on dorsum and forward onto head. No tubercles or spines present on body or tail. Dorsal and lateral surfaces of tail covered in regular rows of small triangular scales (apices directed posteriorly). Ventral surface with smaller, non-aligned rounded scales. Postcloacal sac (housing hemipenes in males) covered in larger rounded scales; sac relatively smaller in females. Cloacal spine cluster of males consists of 6-10 small, conical scales arranged in 2-3 transverse rows; cluster present in females but scales smaller, rounded rather than conical. Preanal region without enlarged scale series or associated pores.

Plantar surface of manus and pes finely granular. Digits moderately elongate, narrowing at level of terminal phalanx, terminating in paired, ovate apical plates. Fine claws project well past end of apical plates, visible to naked eye. Undersurface of digits with small, rounded scales in transverse rows, 2-4 per row.

Head elongate, narrow and moderately deep. Snout distinctly 'beaked', weakly grooved between nostrils. Eye moderately large; supraciliary scales small, triangular except for 2-3 small conical scales at posterior corner of eye. Ear aperture small, horizontally ovate.

Rostral scale high, rectangular, forming anterior border of nostril (Fig 3). Well-defined rostral crease extends ${}^{1}/_{3}$ - ${}^{2}/_{3}$ way towards lip. First supralabial high, forming inferior rim of nostril. Enlarged supranasal scale forms upper rim of nostril, opposing scales usually in broad midline contact but occasionally separated by small internasal scale (*e.g.* R122961). Series of 2-4 small scales complete posterior rim of nostril. Variable number of enlarged scales (0-2) located immediately behind supranasals. Second supralabial about ${}^{1}/_{3}$ height of first. All successive supralabials much smaller, decreasing in size towards oral rictus. Supralabial tally 13-17. First row of loreal scales only slightly smaller than supralabials.

Mental elongate, triangular. First infralabial large, in broad contact with mental and succeeded by 12-13 additional infralabials in decreasing series.

Dorsal pattern variable. Most specimens with 4-5

Table 1

Mensural and meristic data for *Diplodactylus klugei* sp nov and a sample of *D. pulcher* from the southern Carnarvon Basin region. All summary values are mean ± standard deviation. Sexual dimorphism was not present in any dimension so data are pooled for both sexes. *Diplodactylus klugei* is smaller than *D. pulcher* in all dimensions except tail length which is approximately equal in the two species. The ratio data indicate that *D. klugei* is similar in body shape except for having relatively shorter legs. *Diplodactylus klugei* has a significantly higher number of supralabial scales. Values are mean ± standard error with range and/or sample size (n), and with significance of interspecific difference by ANOVA with F-value and probability (P; NS indicates no significance).

	***D. klugei* sp nov**	***D. pulcher***	**ANOVA**
SVL	44.1 ± 6.95 22-55 (n = 49)	50.10 ± 5.81 32-59 (n = 21)	$F_{1,69} = 11.83$ ($P < 0.01$)
Tail	30.13 ± 3.23 23-33 (n = 18)	31.25 ± 6.29 22-36 (n = 4)	$F_{1.21} = 0.18$ (NS)
HeadL	9.51 ± 1.15 6.3-11.3 (n = 48)	10.36 ± 6.71 8.8-11.4 (n = 19)	$F_{1,67} = 8.31$ ($P < 0.01$)
HeadW	7.43 ± 1.03 4.7-9.0 (n = 48)	8.27 ± 0.85 7.1-9.7 (n = 18)	$F_{1,65} = 9.62$ ($P < 0.01$)
TibialL	7.70 ± 1.00 4.5-9.0 (n = 48)	8.70 ± 0.77 6.2-9.6 (n = 21)	$F_{1,69} = 16.58$ ($P < 0.001$)
BifemoralW	17.91 ± 2.01 11.4-20.4 (n = 41)	19.9 ± 2.12 13.9-23.3 (n = 21)	$F_{1,62} = 13.46$ ($P < 0.001$)
Tibial / SVL as %	14.2-19.0 % (n = 7)	15.4-19.4 % (n = 4)	
BifemoralW/SVL as %	34.2-43.9 % (n = 40)	35.9-44.4 % (n = 21)	
Supralabials	14.54 ± 1.18 13-17 (n = 24)	13.10 ± 1.33 11-16 (n = 19)	$F_{1,42} = 14.07$ ($P < 0.01$)

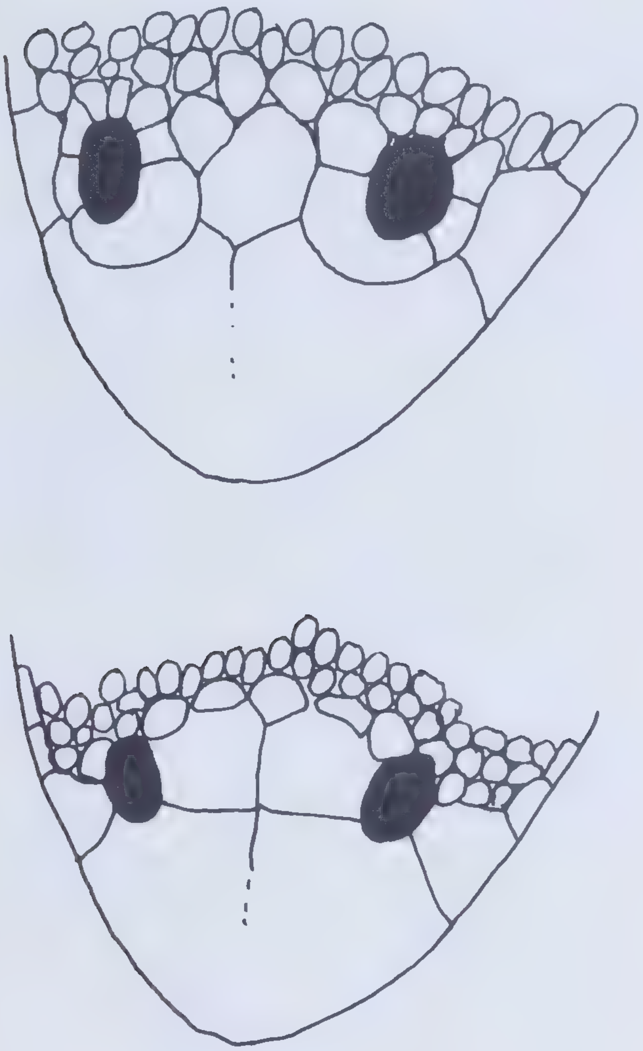


Figure 3. Rostral scalation of *Diplodactylus klugei* sp nov (bottom; WAM R120925) compared with that of *D. pulcher* (top; WAM R126707). Note the diagnostic fusion of prenasal and rostral scales and the absence of an internasal scale in *D. klugei.*

large, pale dark-edged blotches on brown to reddish-brown ground colour (80 % of total sample), but occasional specimens with longitudinal anastomoses between adjacent blotches (8 %; *e.g.* R120925) or with continuous dark-bordered vertebral stripe (12 %; *e.g.* R120884). Flanks pale brown to reddish-brown with irregular pale spots, occasionally interspersed with dark spots (*e.g.* R120941). Tail with 4-5 irregular blotches. Regrown tails lack blotches, usually have irregular dark spotting. Limbs with indistinct pale spotting. Lower flanks and venter immaculate.

Dorsum of head pale brown to reddish-brown, occasionally with darker central spot (*e.g.* R120941). Side of head with broad, pale temporal band which passes through eye to terminate at nostril. Posterior to eye, temporal band bordered below by dark brown to black line or diffuse band which terminates below eye.

Details of holotype

SVL 51mm; Tail 29 mm; HeadL 10.0 mm; HeadW 7.1 mm; TibialL 8.1 mm; BifemoralW 19.3 mm; supralabials 14; supranasals in medial contact. Dorsal pattern a series of irregular, dark-edged blotches. Flanks marked with interspersed pale and dark spots. Single yolked follicle (diameter 7.1 mm) present on each ovary.

Etymology

Named for Professor Arnold Kluge in specific recognition of his contribution to the systematics of the genus *Diplodactylus.*

Distribution

Diplodactylus klugei appears to be confined to the Carnarvon Basin but has a moderately wide distribution within this region (Fig 2). It is recorded from immediately south of Shark Bay north to Giralia and from near coastal localities inland to Mardathuna, Meedo and Woodleigh. It is present on Peron Peninsula but has not been recorded from Edel Land or any of the Shark Bay Islands. Further north, it is present in near coastal habitats on the western margin of Lake Macleod.

Genetic discrimination

Allozyme electrophoresis was conducted with liver samples from five specimens of *D. pulcher* and seven of *D. klugei*. The material selected for analysis comes from two areas where the two taxa were obtained in regional sympatry, *viz.* the Woodleigh and Mardathuna Biological Survey sites. Nine specimens were screened for 41 presumptive loci, with three others scored only for the 13 most informative loci. The individual allele scores for 20 variable loci are shown in Table 2. The following loci were invariant within the initial sample of nine specimens: *Acp1, Acp2, Adh1, Ak1, Alb, Dia, Gapd, Gda, Glo, Got1, Gpi, Gsr, Idh1, Ldh2, Mdh1, Mdh2, Me2, Pgam6, Pk1, Sod* and *Tpi.*

The two taxa show fixed allelic differences at *Acon1, Acyc, PepA* and *Pgm2* and display major differences in allele frequency at six other loci; *Acon2, Est, Gpt, Ihd2, Np* and *Pgm1*. This equates to a genetic distance of 10 % FD or a Nei D of 0.258. Even based solely on the four fixed differences, the odds against the subsamples being drawn at random from a single, freely interbreeding population are exceedingly high (the probability of obtaining no heterozygotes at four loci in a sample of 12 animals drawn at random from a "population" in which each locus has allele frequencies of $p = {}^{5}/_{12}$ and $q = {}^{7}/_{12}$ is $((1-2pq)^{12})^{4}$ or $1.3\ 10^{-14}$). Thus the genetic data strongly support recognition of two distinct biological species within this sample.

Given the broad distributional overlap and high degree of morphological similarity between the two taxa, it is of interest to explore the possibility of hybridization between them. The presence of correlated, fixed allelic differences at four loci makes it quite certain that none of the tested individuals represent F1 hybrids. However, examination of the pattern of heterozygosity between the two taxa does show some interesting features suggestive of possible genetic interaction. In both taxa, the overall level of heterozygosity is very similar ($H_o = 0.120 \pm 0.033$ for *D. pulcher*; $H_o = 0.100 \pm 0.027$ for *D. klugei*), but the distribution of heterozygotes at those loci showing major gene frequency differences between the two taxa is somewhat biased towards *D. klugei* ($H_o = 0.376 \pm 0.079$ *vs*

Table 2

Allozyme profiles of *Diplodactylus pulcher* and *D. klugei* sp nov at 20 variable loci. Code for Carnarvon Basin survey sites; MA = Mardathuna Station, WO = Woodleigh. A dash indicates that the genotype was not determined for this locus.

Specimen Number	Site	*Acon1*	*Acon2*	*Acyc*	*Enol*	*Est*	*Fdp*	*Fum*	*Got2*	*Gpt*	*Idh2*	*Ldh1*	*Mpi*	*Np*	*PepA*	*PepD*	*6Pgd*	*Pgk*	*Pgm1*	*Pgm2*	*Sordh*
D. pulcher																					
R120668	MR3	a	c	cd	b	ac	a	a	a	b	ab	ab	b	b	b	ab	b	a	c	a	b
R120676	MR5	a	cd	d	b	a	a	a	a	b	b	a	b	b	b	ab	b	a	c	a	a
R122756	MR5	a	ce	cd	a	a	-	-	-	-	b	-	b	b	b	-	bc	-	c	a	ab
R120958	WO2	a	cd	cd	ab	a	a	a	ab	b	b	a	bc	b	b	ab	bc	a	c	a	a
R121065	WO2	a	c	d	ab	a	a	a	a	bc	b	a	bc	b	b	b	ab	a	c	a	ab
D. klugei																					
R120715	MR1	b	ab	b	a	b	ab	ab	ab	a	a	a	b	a	a	b	b	a	ab	b	b
R120925	WO4	b	b	b	a	b	a	a	a	ab	a	a	b	a	a	a	b	a	ab	b	b
R120941	WO4	b	bc	b	a	ab	a	ab	a	a	a	a	ab	a	a	a	b	ab	b	b	ac
R120939	WO4	b	bc	b	a	ab	-	-	-	-	a	-	ab	ab	a	-	b	-	b	b	a
R120884	WO4	b	b	ab	a	b	-	-	-	-	a	-	b	ab	a	-	b	-	ac	b	ab
R120881	WO5	b	b	b	a	ab	a	a	a	ab	a	a	b	ab	a	a	b	a	a	b	b
R120870	WO5	b	bc	b	a	b	a	a	a	a	a	a	ab	a	a	a	b	a	b	b	b

$H_o = 0.209 \pm 0.090$ for the loci *Acon2, Est, Gpt, Idh2, Np* and *Pgm1*; Table 2). Because overall levels of heterozygosity do not differ between the taxa, this bias is probably not a product of bottle-necking in *D. pulcher*. Instead, it more likely reflects either chance genetic drift operating on loci which were polymorphic in the ancestral taxon, strong selection operating on certain loci only (either for homozygotes in *pulcher* or for heterozygotes in *klugei*), or a predominantly one-way introgression of *pulcher* alleles into the *klugei* genotype. This issue cannot be resolved with allelic data and will require analysis of mitochondrial genotypes for any further clarification.

Comparison with other species

Diplodactylus klugei is remarkably similar to *D. pulcher* in general morphology (Fig 1A,B). Indeed, were it not for the strong evidence of reproductive isolation provided by the genetic data, the morphological differences might well have been ascribed to polymorphism and local phenotypic variation.

For statistical comparison, the type series of *D. klugei* was compared with a regionally sympatric sample of *D. pulcher* (Table 1). This analysis shows that *D. klugei* is significantly smaller than regionally sympatric *D. pulcher* in all dimensions, and further that it has proportionally shorter limbs. *Diplodactylus pulcher* further differs from regionally sympatric *D. klugei* in the presence of a prenasal scale which excludes both the rostral and the first labial from entering the nostril (Fig 3); a flatter internasal region with the supranasals separated by one or more internasal scales; a slightly lower number of supralabial scales (Table 1); a shorter mental scale in narrower contact with the first infralabial; longer digits with wider apical plates and shorter, nearly-concealed claws; and relatively larger eyes. Although *D. klugei* and *D. pulcher* both occur in blotched and lined pattern morphs, the relative frequency of each within the two taxa is very different. In *D. klugei* only 6 out of 51 specimens bear a simple pattern of parallel longitudinal lines, contrasting with 18 out of 23 specimens of the regionally sympatric sample of *D. pulcher*. Four other specimens of *D. klugei* show an intermediate pattern where the more characteristic blotches are united by a verterbal stripe.

Diplodactylus pulcher has an extensive distribution outside of the Carnarvon Basin, covering much of Western Australia except for the southern and the north-eastern regions (Fig 4). The WA Museum holds a total of 430 specimens of *D. pulcher*, which have been examined as part of an ongoing study of geographic variation in this species. In the present context, the most important finding is that *D. pulcher* consistently has separate prenasal scales throughout its range and almost always has one or more internasal scales. In contrast, the frequency of blotched *vs* lined pattern variants shows significant geographic variation, with a higher frequency of blotched individuals in southern populations of *D. pulcher*. Likewise, digit lengths and terminal pad size and relative limb lengths are subject to significant geographic variation in *D. pulcher*. *Diplodactylus klugei* is thus reliably distinguished from *D. pulcher* as a whole only on the basis of rostral scalation features, although dorsal pattern and limb

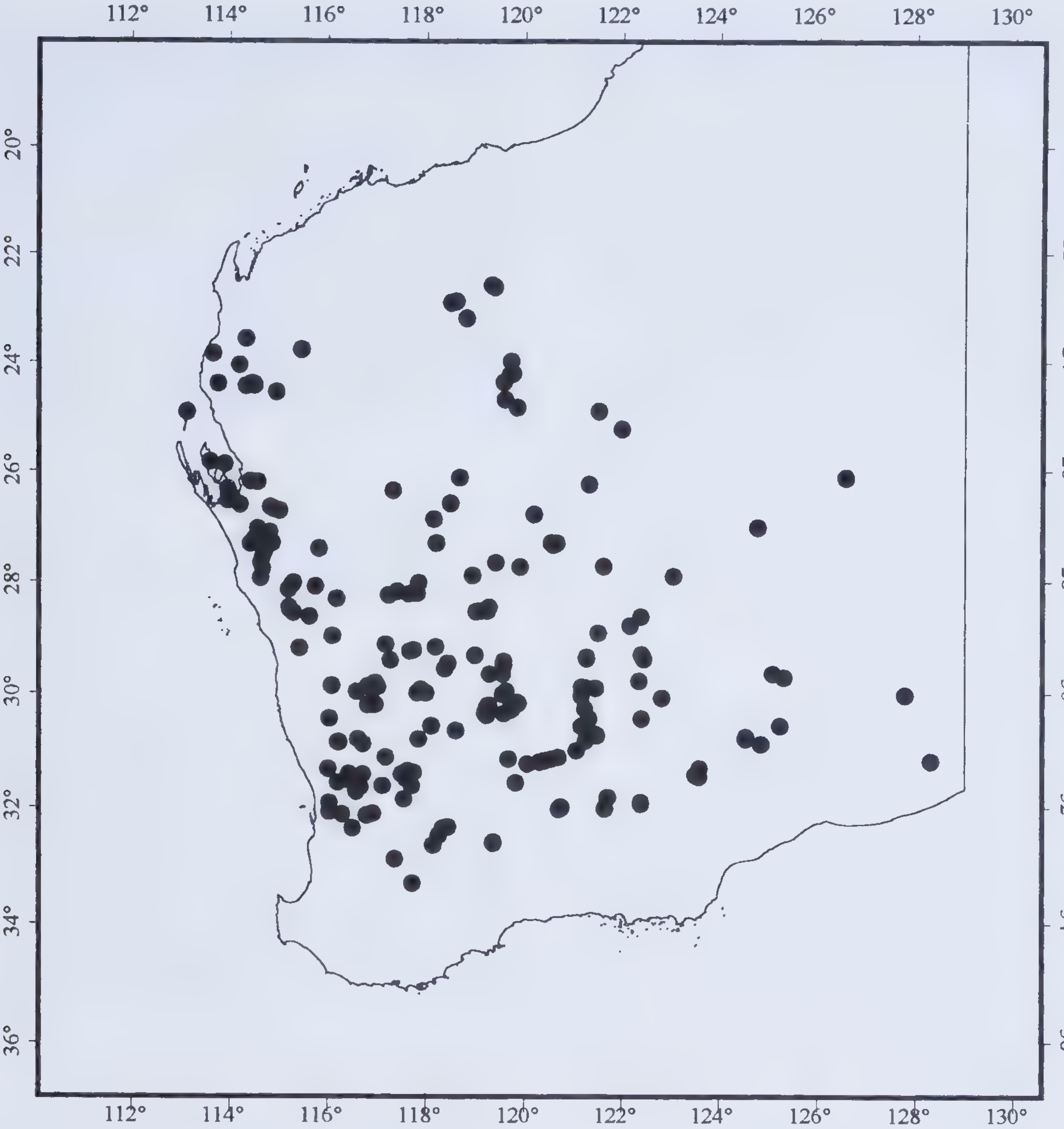


Figure 4. Distribution of *Diplodactylus pulcher* in Western Australia.

proportions provide a supplementary guide to identity in the case of Carnarvon Basin specimens.

Kluge (1967) regarded *D. pulcher* to be an isolated species without close relatives. He included it within his *vittatus* group but noted that it might also have links to the *conspicillatus* group based on the shared reduction of the labial scales. Both *Diplodactylus klugei* and *D. pulcher* show a superficial similarity in body patterning to *D. galeatus* Kluge of the Central Australian highlands and *D. steindachneri* Boulenger of Eastern Australia, but they differ from these species in various features including the greater degree of reduction of the labial scales. To date, there has been no comprehensive phylogenetic analysis of the genus *Diplodactylus* and very little comparative genetic analysis against which to evaluate the results of the present investigation.

Taxonomic remarks

Cogger *et al.* (1993) list three taxa as synonyms of *D. pulcher*. The most important of these in the present context is *Diplodactylus lucasi* Fry (a replacement name for *Diplodactylus bilineatus* Lucas and Frost). The holotype of *Diplodactylus bilineatus* Lucas and Frost (MOV D7570) is accompanied by a label with the following information: Minilya, 80 miles inland from Carnarvon Well, 9.5.1903, D.T. Wall / "TYPE" on rear. The specimen is of adult size and appears to be a female based on the size of the postcloacal spines and sac. According to Kluge (personal communication, 1997), the specimen was in a reasonable condition when he examined it in the mid-1960s; he reported that the rostral and first supralabial scales of MOV D7570 were both excluded from the nostril (Kluge 1963), a character of *D. pulcher* as restricted here. Unfortunately, the holotype is now very dehydrated and brittle and the critical scale boundaries are no longer visible on the rostrum. As suggested by the original specific epithet, MOV D7570 has the strongly lined dorsal pattern seen in the majority of Carnarvon Basin *D. pulcher*, but a comparable condition is also present in a minority of *D. klugei*. Features more reminiscent of *D. klugei* include an elongate mental in extensive contact with the first infralabial and long claws which protrude beyond the apical plates on all digits (the latter character might reflect shrinkage of the apical pads). Minilya is on the eastern side of Lake Macleod, and both *D. pulcher* and *D. klugei* could be expected to occur in the general vicinity.

The apparent admixture of both *pulcher* and *klugei* characters in the holotype of *bilineatus* is perhaps what might be expected of a hybrid individual. If this is indeed so, *D. bilineatus* Lucas and Frost would be unavailable under the terms of Article 23h of the International Code for Zoological Nomenclature (Anon 1985) which disallows individuals of hybrid origin as holotypes of species-level taxa. However, for the present, we are inclined to treat *D. lucasi* Fry as a junior subjective synonom of *D. pulcher*, based principally on Kluge's record of the rostral scalation at a time when the specimen was in better condition.

The lectotype of *Stenodactylopsis pulcher* Steindachner (from ' Swan River, WA' = hinterland of Perth) and holotypes of *Diplodactylus pulcher dorsotaeniata* Pellegrin (from 'Birrigrin, WA' = 50 km NE of Sandstone) and *Diplodactlyus pulcher dorsalis* Werner (from Eradu, WA) have not been examined during this study. However, we have examined near-topotypic specimens for each of these forms and believe in each case that they can be accomodated within a single, geographically variable species. On present evidence, we thus find no grounds to support Wells & Wellington's (1983, 1985) otherwise unsubstantiated resurrection of *D. lucasi* and *D. dorsalis* from synonymy of *D. pulcher*.

Habitat and sympatry

Diplodactylus klugei clearly occupies a variety of different habitats. Specimens collected during the Biological Survey were obtained from samphire on the edge of Lake Macleod, from the floodplain of the Wooramel river, from the margin of a claypan on Meedo and from *Acacia grasbyi* shrubland on calcareous soils on Woodleigh. A common factor among these localities appears to be the presence of relatively hard, loamy soils rather than looser sands. In contrast, Biological Survey capture records of *D. pulcher* indicate a preference for sandier substrates either on dunes or in sandplain habitats. However, certain of the earlier records of *D. klugei* come from areas of predominantly sandy rather than loamy substrates (*e.g.* 5 km SE of Gnaraloo, Warroora, Giralia) and *D. pulcher* is known to occupy a wide variety of habitat types across its extensive geographic range.

Although *D. klugei* and *D. pulcher* are regionally sympatric over quite a large area, the two species were not found to co-occur on any of the Biological Survey quadrats. On Mardathuna, for example, *D. pulcher* was captured on quadrats MR2-5 while *D. klugei* was obtained exclusively on MR1. Similarly on Woodleigh, *D. pulcher* was obtained on quadrat WO2, and *D. klugei* on quadrats WO4-5. Further, more specific field studies are required to determine the extent and basis of any habitat partitioning between these morphologically similar geckos in the southern Carnarvon Basin.

During the Biological Survey, *Diplodactylus klugei* was obtained from the same quadrats as *D. squarrosus*, *D. stenodactylus*, *D. conspicillatus* and *D. strophurus*. *Diplodactylus pulcher* was found together with this same suite of congenors and additionally with *D. alboguttatus*.

Family Scincidae

Ctenotus maryani sp nov

(Fig 5A)

Holotype

R126761 in the Western Australian Museum, an adult male collected on 18/3/96 at Biological Survey Quadrat MR2, 5.6 km W of Mardathuna Homestead, WA, in 24° 26′ 36″ S 114° 30′ 43″ E (Fig 6).

Paratypes

15 km NE Giralia HS (22° 22′ S, 114° 29′ E): 61185; 3 km E Giralia HS (22° 41′ S, 114° 24′ E): 61121-2, 61147; 14 km N Marrilla HS (22° 51′ S, 114° 27′ E): 61255; 4 km W Barradale Roadhouse (22° 51′ S, 114° 55′ E): 80299; 0.5 km SE Merlinleigh HS (24° 19′ S, 115° 11′ E): 99636; **MR4**, 11.8 km W Mardathuna HS (24° 24′ 26″ S, 114° 28′ 24″ E): 120802, 122777, 126774; **MR3**, 7.7 km W Mardathuna HS (24° 25′ 44″ S, 114° 29′ 60″ E): 121555, 122735, 125364; **MR2**, 5.6 km W Mardathuna HS (24° 26′ 36″ S, 114° 30′ 43″ E): 120685; **KE1**, 41 km from Binthalya HS (24° 29′ 36″ S, 115° 01′ 51″ E): 120530; 9 km NNW Carey Downs HS (25° 32′ S, 115° 26′ E): 114313.

Diagnosis

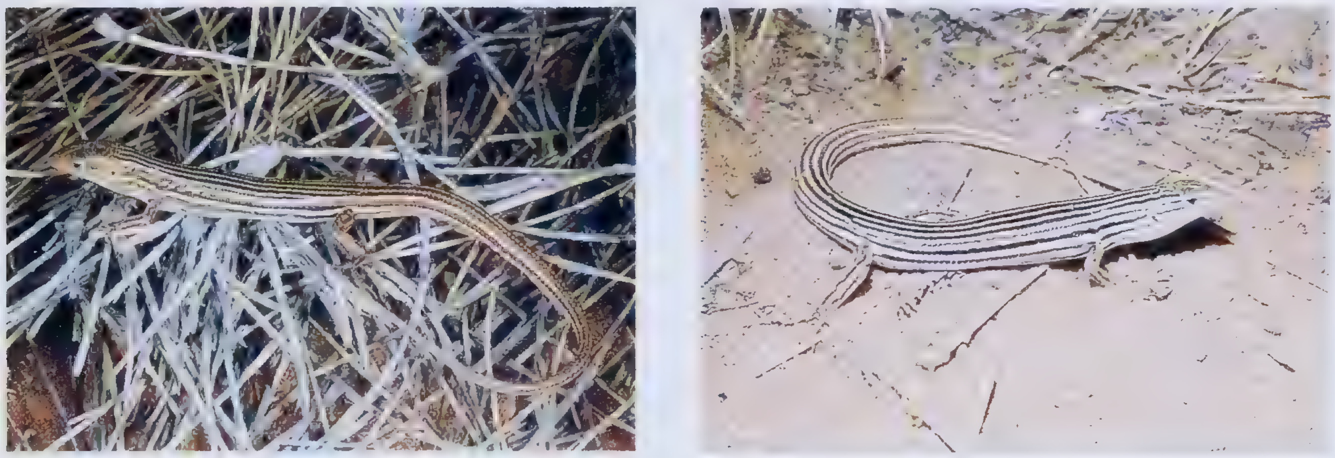
A medium-sized *Ctenotus* with pattern 'simple', comprising eight to ten pale stripes on a dark-brown to reddish-brown ground colour; body with 26-28 midbody scale rows; digits of manus and pes with keeled and weakly mucronate subdigital lamellae, 14-17 on manal digit III and 24-26 on pedal digit IV; ear lobules triangular, numerous and subequal; dorsal and lateral pattern terminating on neck, dorsum and temporal region of head with indistinct, irregular mottling only; legs with irregular and poorly-developed reticulum.

Description

A relatively slender-bodied, long-limbed *Ctenotus* with a predominantly 'simple' pattern of alternating pale and dark stripes. No sexual dimorphism in body size, proportions or colouration. SVL to 54 mm; Tail to 119 mm; ForelimbL to 14.9 mm; HindlimbL to 23.9 mm.

Paravertebral scales 51-62, mean. = 55.8 ± 3.3 (sd); scales in 26-29 rows at midbody, modal count 28 (41% of sample). Other mensural and meristic data are given in Table 3.

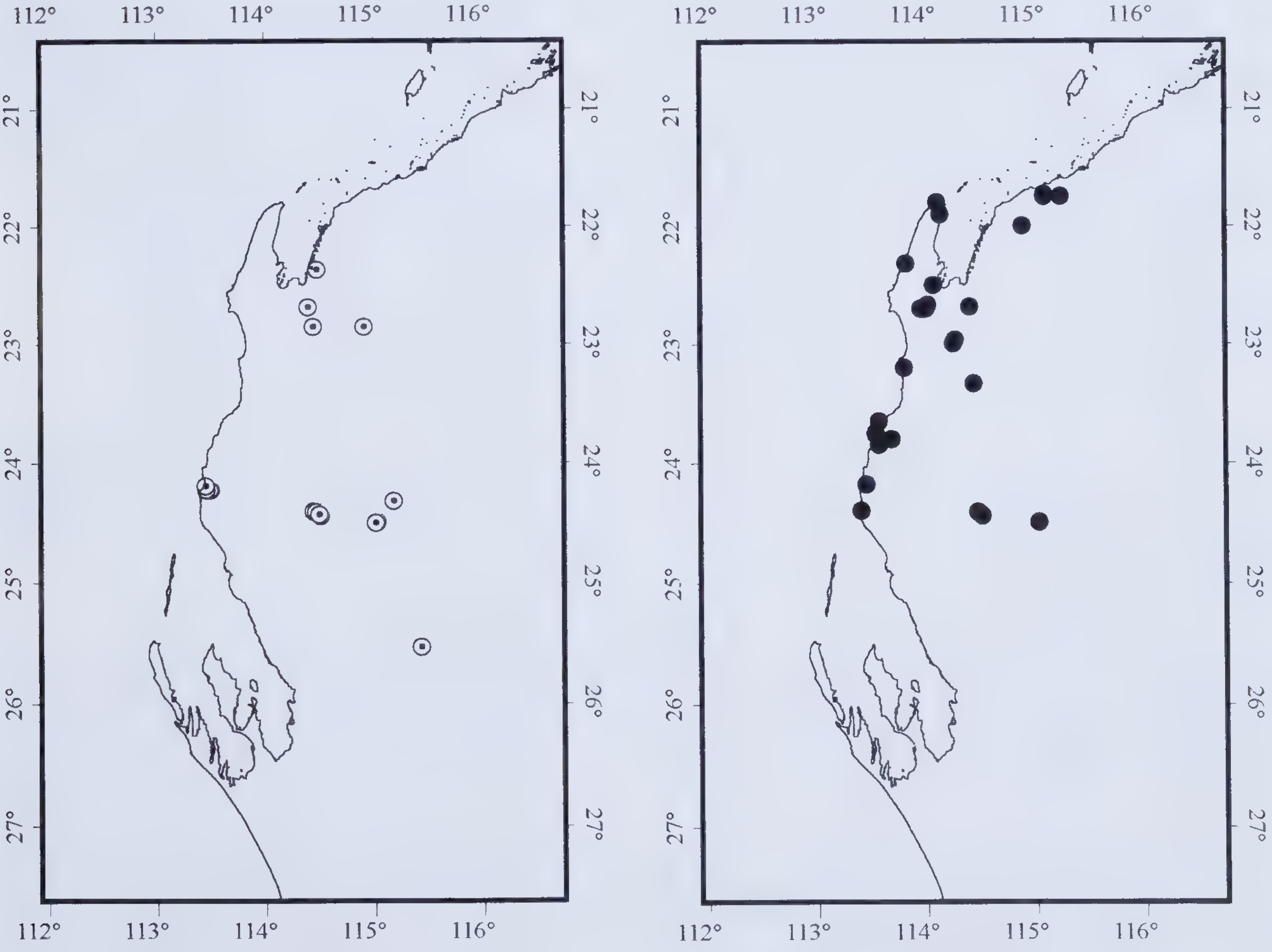
Plantar surface of manus and pes spinose, unpigmented. Digits slender, relatively elongate,



A. *Ctenotus maryani*

B. *Ctenotus iapetus*

Figure 5. Individuals of *Ctenotus maryani* sp nov. and *C. iapetus* Storr, illustrating the remarkable similarity of these genetically quite distinct species. Details of specimens as follows; *Ctenotus maryani* sp nov, WAM R114313, an adult male from 9 km NNW Carey Downs Homestead, photographed by B Maryan; *C. iapetus*, WAM R51018, an adult female from 3 km NW Bullara Homestead, photographed by R E Johnstone.



C. *maryani*

C. *iapetus*

Figure 6. Distribution of *Ctenotus maryani* sp nov and *C. iapetus* in the Carnarvon Basin region of Western Australia. Both species are endemic to the region.

Table 3

Mensural and meristic data for *Ctenotus maryani* sp nov and *C. iapetus*. All values are mean ± standard deviation, followed by range and sample size. Sexual dimorphism was not present in any dimension so data are pooled for both sexes. *Ctenotus iapetus* evidently attains a larger overall size than *C. maryani* but sample means for SVL are not significantly different. *Ctenotus maryani* has a significantly higher mean number of paravertebral scales than does *C. iapetus*. The ratio data indicate that *Ctenotus maryani* has relatively shorter limbs than *C. iapetus*. Values are mean ± standard error with range and/or sample size (n), and with significance of interspecific difference by ANOVA with F-value and probability (P; NS indicates no significance).

	C. maryani	*C. iapetus*	ANOVA
SVL	47.56 ± 6.55 33-54 (n = 18)	49.20 ± 11.76 31-68 (n = 82)	$F_{1,99}$ = 0.326 (NS)
Tail	98.80 ± 19.98 64-119 (n = 10)	95.84 ± 24.61 60-149 (n = 44)	$F_{1,53}$ = 1.341 (NS)
ForelimbL	12.62 ± 1.77 8.1-14.9 (n = 18)	13.89 ± 2.59 8.9-18.1 (n = 81)	$F_{1,98}$ = 3.88 (NS)
HindlimbL	21.31 ± 2.43 14.8-23.9 (n = 18)	23.23 ± 4.47 15.5-31.0 (n = 77)	$F_{1,94}$ = 3.11 (NS)
Tail/SVL * 100	179-236 %	163-244 %	
ForelimbL/SVL*100	22.5-29.4 %	22.3-37.9 %	
HindlimbL/SVL*100	40.4-52.1 %	39.9-60.6 %	
PV	55.83 ± 3.31 51-62 (n = 18)	50.91 ± 2.90 44-61 (n = 70)	$F_{1,87}$ = 38.79($P < 0.001$)
SDL-M3	16.0 ± 0.71 15-17 (n = 9)	15.66 ± 1.22 13-18 (n = 77)	$F_{1,85}$ = 0.668 (NS)
SDL-P4	25.22 ± 1.31 21-26 (n = 18)	26.17 ± 1.63 23-30 (n = 77)	$F_{1,94}$ = 5.288 (NS)

terminating in fine claw. Subdigital lamellae keeled and with small mucrons. SDL 14-17 on manal digit III, modal count 16 (56 % of sample); 24-26 on pedal digit IV, modal count 26 (61 % of sample).

Nasals and prefrontals both in broad medial contact. Loreals 2, anterior higher but less elongate than second (Fig 7). Supralabials 8-9, 5 or 6 of these making up discrete preorbital series. Postsupralabials [postlabials of Taylor (1935)] 2. Infralabials 8. Supraoculars 4, second wider than third, all but last in contact with frontal (Fig 8). Supraciliaries 7-8, either 1>2>3>>4-7 with anterior 3 in contact with first supraocular, or 1>2>>3-8 with anterior 4 in contact with first suprocular. Eyelid mobile, with three enlarged scales forming a divided window. Preoculars 2 [lower is anterior presubocular of Taylor (1935)]. Single presubocular, wedged between supralabials 5-6 or 6-7. Postsuboculars 3, abutting penultimate supralabial and primary temporal, in series with pretemporals. Single primary temporal, wedged between last two supralabials. Secondary temporals 2, upper much larger than lower. Frontoparietal larger than interparietal. Parietal eye clearly visible at rear of interparietal. Parietals in contact behind interparietal. Nuchals in 2-4 pairs, 83 % with 4 nuchals on at least one side.

Ear aperture moderately large. Usually with 2-3 large triangular lobules, bordered above and below by one or more smaller, rounded lobules (Fig 7).

Ground colour of body dark-brown on dorsum, paler reddish-brown on flanks. Dorsum with four continuous stripes (Fig 9); white paravertebral stripe (positioned centrally on SR-1), off-white dorsal stripe (centre SR-2), white dorsolateral (centre SR-3) and off-white upper lateral (lateral SR-4). Flank always with broad midlateral and lower lateral stripes; both are white, positioned on scale rows 6 + part 7 and 8 + part 9 respectively. Lower lateral stripe faintly delineated below by thin brown line (centre SR-9). Upper lateral zone variable: either solid brown, covering whole of SR-5 and intercalcating tips of rows 4 and 6 (*e.g.* R80299, R121555) or divided by off-white accessory upper lateral stripe (centre SR-5). Accessory stripe usually indistict, comprised of irregular

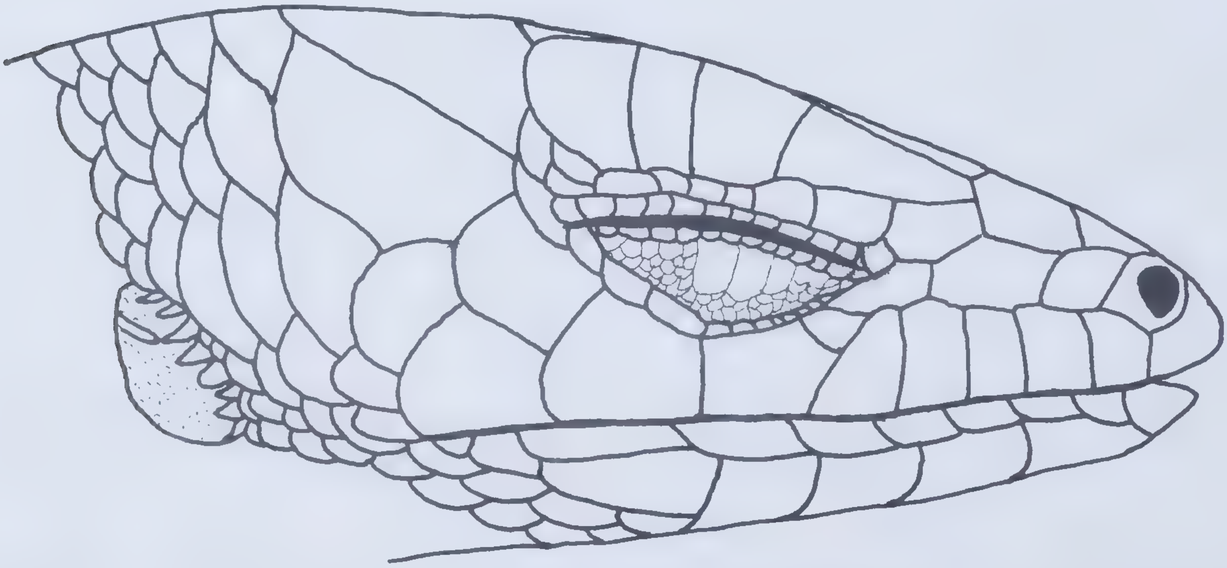


Figure 7. Scalation of the lateral surface of the head of *Ctenotus maryani* sp nov (WAM R126761).

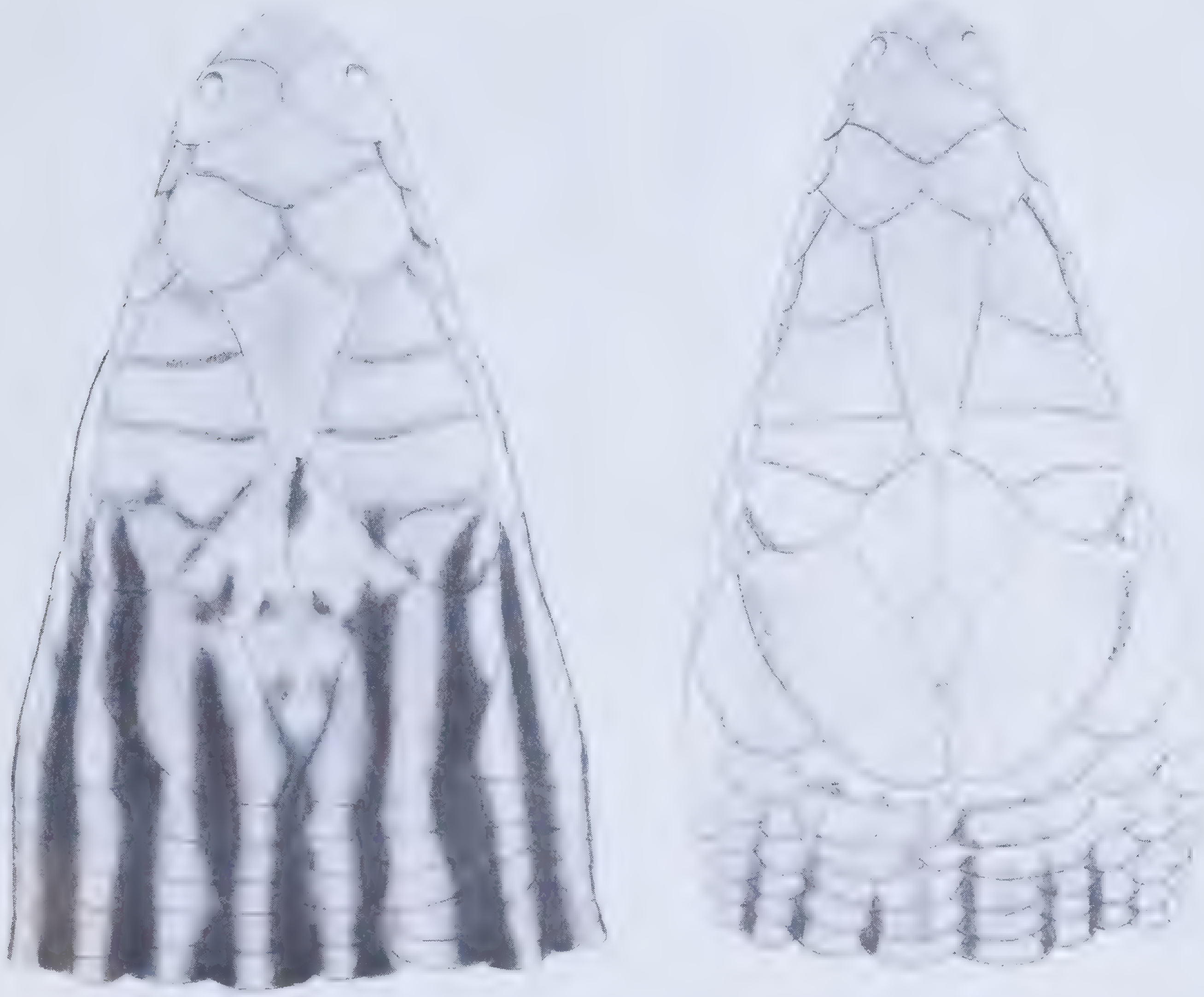


Figure 8. Scalation and patterning of the dorsal surface of the head and neck in *Ctenotus iapetus* (left; WAM R122921) and *C. maryani* sp nov (right; WAM R126761). Note the diagnostic discontinuation of the dorsal pattern at the level of the nuchal scales in *C. maryani*, compared with the continuation of dorsal patterning onto the parietal and frontoparietal scales in *C. iapetus*.

dashes (*e.g.* R114313, R126756, R126761), but occasionally continuous and well-defined (*e.g.* R120685).

Dorsal pattern terminates at level of nuchal scales (Fig 8). Lateral pattern extends forward of forelimb to terminate at level of ear aperture, ringed in white. Dorsum and sides of head pale brown, indistinctly marked as follows: lower temporal and postlabial scales with irregular white blotches; upper temporal scales and parietal scales with white flecking between eye and each of dorsal and dorsolateral stripes; subocular region with faint white streak; most scales and lower margin of orbital fossa with fine dark-brown emargination.

All pattern elements except dorsal stripe extend onto tail but with reduced intensity; tail paler than dorsum. Limbs with longitudinal dark-brown stripes, with occasional reticulation, extending onto digits. Venter immaculate throughout.

Details of Holotype

SVL 51 mm; Tail 118 mm; ForelimbL 15 mm; HindlimbL 24 mm; paravertebral scales 53; midbody scale rows 26; subdigital lamellae manus III 15; subdigital lamellae pes IV 25; supralabials 8; supraciliaries 8; upper ciliaries 10; ear lobules 4 on right, 3 on left; nuchals 3 pairs. Upper lateral zone with weakly defined accessory pale stripe. Testis regressed, efferent duct turgid.

Etymology

Named for Mr Brad Maryan, irrepressible enthusiast of the Australian herpetofauna, outspoken advocate of amateur reptile-keeping and a major contributor to the herpetological collections of the Western Australian Museum.

Distribution

Apparently restricted to the central and northern parts of the Carnarvon Basin, from the vicinity of Carey Downs HS, inland to the Kennedy Range and north to Giralia (Fig 6).

Genetic discrimination

Ctenotus maryani was compared genetically with *C.*

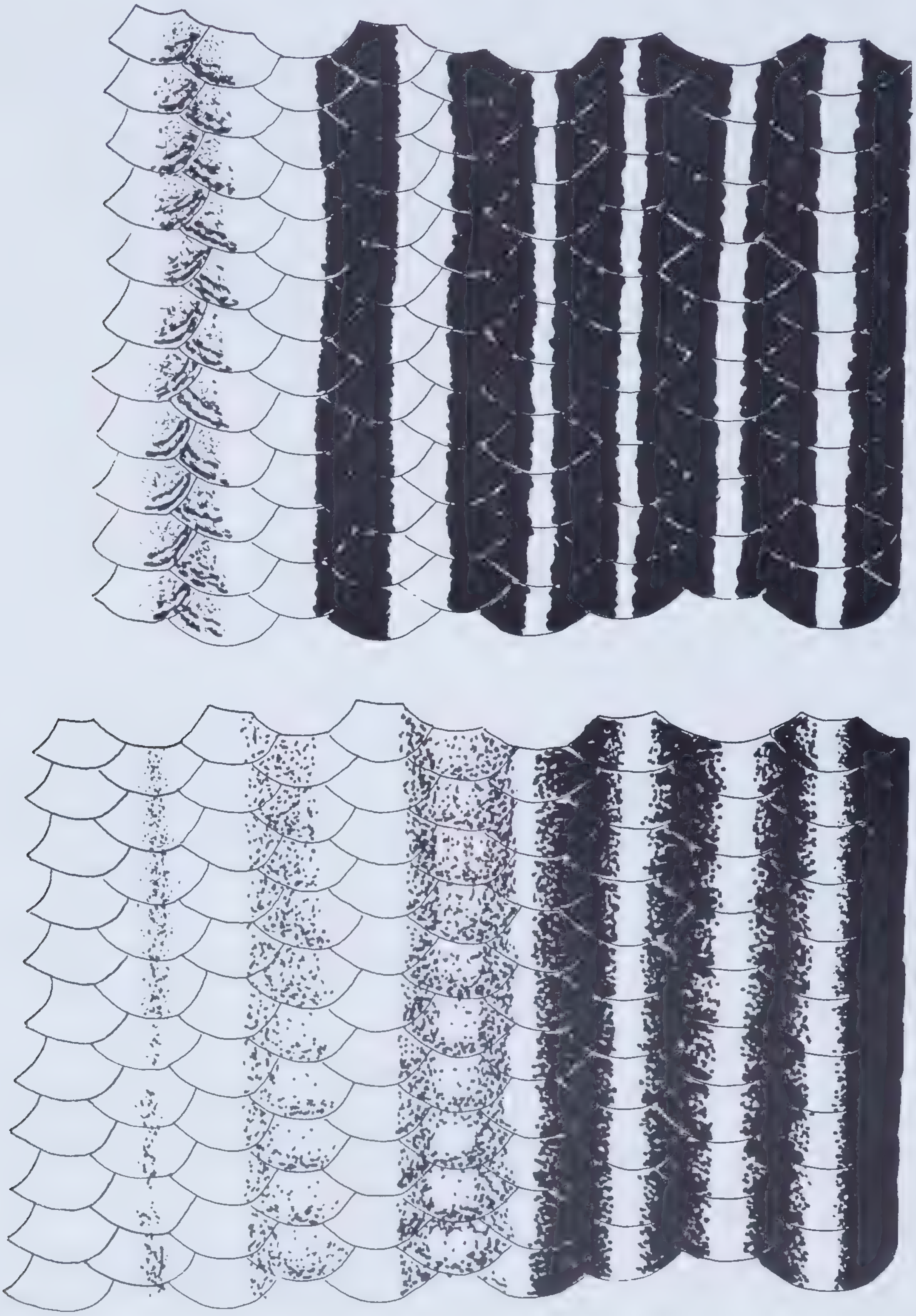


Figure 9. Semi-schematic diagram of the dorsal and lateral body pattern of *C. iapetus* (top; WAM R122911) and *Ctenotus maryani* sp nov (bottom; WAM R126761). The pattern is illustrated relative to the boundaries of longitudinal scale rows. The right hand margin corresponds with the dorsal midline.

iapetus Storr, the species with which it formerly was confused. *Ctenotus maryani* is morphologically quite distinct from all other species of the genus, hence broader genetic comparisons were not required to justify specific recognition.

A total of 10 individuals was screened at 46 presumptive loci. The sample comprised seven individuals of *C. iapetus* and three of *C. maryani*. The three individuals of *C. maryani* came from quadrats MR3 and MR4 on Mardathuna and quadrat KE1 on the slopes of the Kennedy Range. The seven individuals of *C. iapetus* included two from each of these sites and one

Table 4

Allozyme profiles of *Ctenotus iapetus* and *C. maryani* sp nov at 23 variable loci. Code for Carnarvon Basin survey sites: MR = Mardathuna Station, KE = Kennedy Range. A dash indicates that the genotype was not assignable at this locus due to poor sample activity.

Specimen Number	Site	*Acon1*	*Acon2*	*Adh1*	*Alb*	*Ca*	*Est2*	*Fdp*	*G6pd*	*Gapd*	*Got1*	*Hbdh*	*Idh1*	*Ldh*	*Me*	*PepA*	*PepB*	*PepD 1*	*PepD 2*	*6Pgd*	*Pgm*	*Pk2*	*Sod*	*Tpi*
C. iapetus																								
R123186	KE1	-	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	a	b	b	b	ab	a	b
R123187	KE1	a	b	b	b	a	b	a	b	a	ab	b	b	a	b	c	a	b	b	b	b	a	a	b
R122838	MR2	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	b	b	b	b	a	ab	b
R122725	MR3	ab	ab	b	b	a	b	a	b	a	a	b	b	a	b	c	a	b	b	b	b	a	a	b
R122728	MR3	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
R120375	MR4	a	b	b	b	a	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
R120698	MR4	a	b	b	b	ab	b	a	b	a	a	b	b	a	b	c	a	ab	b	b	b	a	a	b
C. maryani																								
R120530	KE1	a	ab	a	a	a	a	ab	a	b	a	a	a	b	a	b	b	b	a	a	b	ab	a	a
R122735	MR3	a	b	a	a	a	a	a	a	b	a	a	a	b	a	bc	b	b	a	a	ab	-	a	a
R120802	MR4	a	b	a	a	a	a	a	a	b	a	a	a	b	a	ab	b	b	a	a	b	a	a	a

from quadrat MR2 on Mardathuna. The sample is thus drawn from within an area of broad distributional overlap between the two taxa and includes material obtained in immediate sympatry.

Of the 46 loci examined, the following 23 were invariant; *Acp1, Acp2, Acyc, Adh2, Ak1, Dia, Enol, Est1, Fdp, Fum, Gda, Glo, Got2, Gpi, Gsr, Idh2, Mdh1, Mdh2, Mpi, Np, Pgam, Pgk* and *Srdh*. The allozyme profiles of all 10 individuals at the 23 variable loci are shown in Table 4.

The two taxa show fixed allelic differences at 13 loci; *Adh1, Alb, Est2, G6pd, Gapd, Hbdh, Idh1, Ldh1, Me2, PpB, PpD2, 6Pgd* and *Tpi*. This equates to a genetic distance of 28% FD or a Nei D of 0.328. The level of heterozygosity is very low in both species (H_o = 0.047 ± 0.021 for *C. maryani*; H_o = 0.028 ± 0.012 for *C. iapetus*) with the majority of loci having a single allele or one allele for each taxon. Accordingly, only one additional locus, *PepA*, displays a major difference in allele frequency between the two taxa. No obvious genetic differences exist between the two localities within either taxon.

The high level of genetic differentiation which exists between sympatric populations of *C. maryani* and *C. iapetus* amply confirms that that the two represent distinct biological species. Moreover, it gives cause for speculation that these species may not in fact represent true siblings, but might each be more closely related to some other taxon or cluster of taxa within the genus (see below).

Comparison with other species

Ctenotus maryani will be compared first with the sympatric *C. iapetus*, then with other small to medium-sized *Ctenotus* with 'simple' patterns and smooth to obtusely keeled subdigital lamellae (members of Storr *et al.*'s (1981) *Ctenotus atlas* group).

Ctenotus iapetus attains a larger size than *C. maryani* and has a heavier build and slightly longer-limbs (Table 3). It has a lower modal midbody scale count (26 *vs* 28 in *maryani*) and a significantly lower paravertebral scale count (Table 3). The digits of *C. iapetus* appear slightly longer and the subdigital lamellae have less prominent keels with smaller mucrons than those of *C. maryani*. *Ctenotus iapetus* typically has 2-3 pairs of nuchal scales (usually 4 pairs in *C. maryani*).

Although the body pattern is superficially similar in the two species, there are a number of significant differences (Fig 5A,B). In *C. iapetus* the longitudinal stripes are brilliant white and form a bold contrast with the uniform dark-brown to black ground colour; furthermore the dorsal and lateral stripes continue forward onto the dorsum and pretemporal regions of the head (the midlateral stripe passing below the eye to extend along the upper lip). In contrast, the pattern of *C. maryani* is more subdued, the variably white to off-white longitudinal stripes being less prominent against a dark-brown to reddish-brown ground colour, and the body pattern fading into an irregular mottling on the neck and head. The limbs in *C. iapetus* are also more boldly and regularly striped.

Ctenotus maryani and *C. iapetus* are both restricted to the Carnarvon Basin region, although the range of *C. iapetus* extends further north onto the Cape Range Peninsula and Onslow coastal plain (Fig 6).

Ctenotus quattuordecimlineatus (Sternfeld) of the central and northwestern Australian sand deserts is very similar to *C. iapetus* (see further comments below), hence it differs from *C. maryani* in essentially the same features which distinguish the latter species from *C. iapetus*. However, *C. quattuordecimlineatus* attains an even larger size (SVL to 70 mm), has a more sharply-defined reticulate (rather than lined) pattern on its limbs, and has a continuous, better-defined accessory upper lateral stripe (generally absent or weakly indicated in *C. maryani*). In some individuals of *C. quattuordecimlineatus*, a further incomplete stripe or row of dashes extends back from the axilla within the lower lateral zone, making a total of eight white stripes on each side compared with a maximum of seven in *C. maryani*.

Ctenotus ariadnae Storr of central Western Australia is readily distinguished from *C. maryani* by the strong black marbling of the frontoparietal and temporal regions. It also has a higher number of midbody scale rows (28-34) and longer digits with more finely keeled and mucronate subdigital lamellae. In adult *C. ariadnae*, the lateral pattern consists of numerous fine stripes anteriorly, breaking up into irregular spotting posteriorly. In juveniles, a more regular pattern of fine stripes is evident, with a continuous pale stripe running down the centre of each of SR-1 to SR-9.

Of the remaining members of Storr's *Ctenotus atlas* group, *C. atlas* Storr and *C. leae* (Boulenger) are similar to *C. maryani* in the absence of strong facial patterning, but each is readily distinguished on other criteria; *Ctenotus atlas* by its fewer pale stripes (maximum of 5 on each side) and higher number of midbody scales rows (28-34); and *C. leae* by its fewer pale stripes (3 on each side), generally fewer midbody scale rows (21-26), and larger presubocular and loreal scales (hence lower, more rectangular, anterior supralabials).

Ctenotus zastictus Storr, currently known only from an isolated patch of eucalpyt-*Triodia* habitat south of Shark Bay, is overall quite similar to *C. maryani* in limb and body proportions, head scalation and body pattern. It differs from *C. maryani* in having interrupted (*i.e.* dashed) rather than continuous dorsolateral and midlateral stripes, more regularly striped legs and a slightly lower midbody scale count (24-26). Storr (1984) noted the close resemblance between *C. zastictus* and *C. iapetus* (*sensu lato*) and referred both to his *C. atlas* species-group. His observations may have been due in part to confusion between *C. iapetus* and *C. maryani*.

Habitat and sympatry

In the Kennedy Range *C. maryani* was obtained from a red dune crest with a tall shrub layer of *Grevillea, Acacia* and *Banskia* over *Triodia*. On Mardathuna it occurs both on red dune and on red sand plain habitats, with *Acacia* woodland over *Plectrachne*. In the north (Giralia, Barradale & Merlinleigh) it appears to be associated specifically with interdune habitats with *Triodia*. On Carey Downs it was collected from *Triodia* beneath *Acacia* on 'fairly hard clay red soil' (notes accompanying specimen R114313). A specific association with hummock grasses may be reasonably inferred from its known distribution.

Ctenotus maryani is found in local sympatry in the Kennedy Range with *C. iapetus, C. pantherinus* and *C. rufescens*. On Mardathuna it is locally sympatric with these species and with *C. hanloni* and *C. piankai*.

Other remarks

Ehmann (1992: 202) figured an individual of *Ctenotus maryani* as *C. iapetus* but did not provide locality details. True *C. iapetus* has been illustrated by Storr *et al.* (1981; Plate 8.2) and by Wilson & Knowles (1988:362).

Removal of *C. maryani* from within *C. iapetus* makes it necessary to reconsider the relationship between the latter taxon and *C. quattuordecimlineatus*. Storr (1975) initially described *iapetus* as a subspecies of *C. quattuordecimlineatus* but later elevated the taxon to species level without comment (Storr & Hanlon, 1980). Interestingly, this action was taken following collection of the first specimens of *C. maryani* by Harold, Hanlon and others around Giralia and after examination of this new material in preparation for publication of "Lizards of Western Australia I. Skinks" (Storr *et al.* 1981; their account of *C. iapetus* is clearly based on a 'mixed' sample). Thus Storr's decision to dissociate *iapetus* from *quattuordecimlineatus* may have been influenced to some extent by characteristics of *C. maryani*. Interestingly enough, Cogger (1992; also Cogger *et al.* 1983) has continued to list *iapetus* as a subspecies of *quattuordecimlineatus*, which is mapped with a continuous distribution from Cape Range through to central Australia. Examination of WA Museum records indicates that the distribution is actually disjunct, with a gap of several hundreds of kilometers between the nearest specimens of *iapetus* and *quatturodecimlineatus*.

Preliminary morphological comparisons of *C. iapetus* (*sensu stricto*) with topotypic material of *C. quattuordecimlineatus* suggests that these taxa probably are closely related. Nevertheless, *iapetus* differs from *quattuordecimlineatus* in usually lacking any trace of an accessory dorsolateral stripe, and in having more boldly striped limbs and longer digits with higher subdigital lamellar counts. For the present, therefore, we prefer to maintain them as distinct species pending more detailed morphological and genetic studies of this group. Greer (1992) also favours recognition of two species.

Menetia surda cresswelli subsp nov

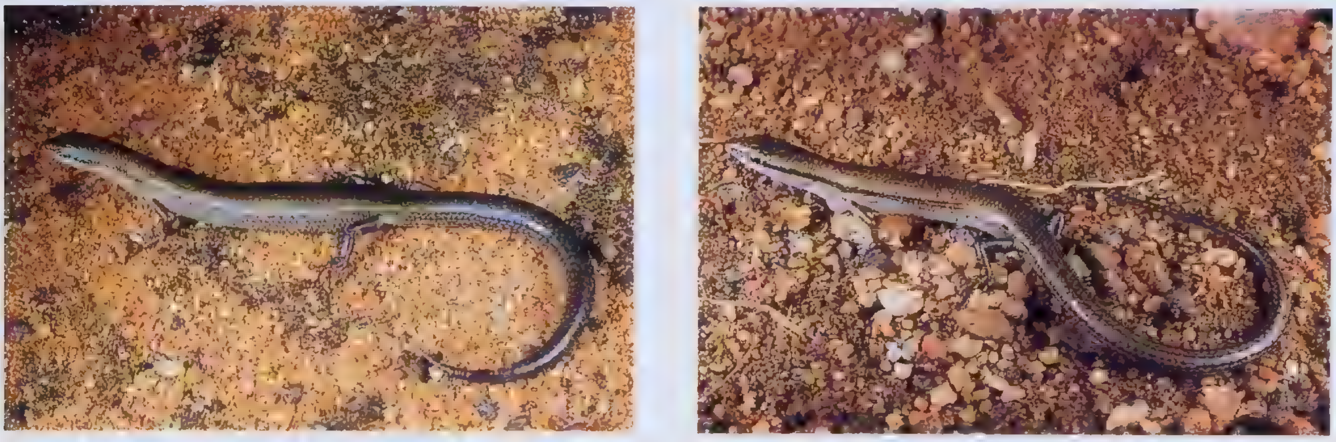
(Fig 10A)

Holotype

R101249 in the Western Australian Museum, an adult male collected by M Peterson on 25/5/1987 at 19 km N Yuna, WA, in 28° 10′ S, 115° 03′ E (Fig 11).

Paratypes

Bernier Island (24° 46′ S, 113° 09′ E): 20524-5; **PE2**, 3 km SSW Peron HS (25° 52′ 31″ S, 113° 33′ 01″ E): 121653; **PE5**, 13.5 km S Peron HS (25° 58′ 33″ S, 113° 34′ 16″ E): 121647-48, 123620, 123678-79; 25 km S Denham (26° 06′ S, 113° 37′ E): 54573-8, 54826; 8 km SE Nanga HS (26° 17′ S, 113° 51′ E): 54901-05; 12 km SW Hamelin HS (26° 29′ S, 114° 05′40″ E): 92465; **NA2**, 16 km SW Hamelin HS (26° 29′ 23″ S, 114° 03′ 21″ E): 120780; 48 km W Overlander Roadhouse (26° 30′ S, 114° 02′ E): 64358, 64367; 27 km E Tamala HS (26° 32′ S, 113° 56′ E): 18471; **NA4**, 27 km SW Hamelin HS



A. *Menetia surda cresswelli*

B. *Menetia surda surda*

Figure 10. Individuals of *Menetia surda cresswelli* subsp nov and *Menetia surda surda* Storr, illustrating the differences in body patterning between these morphologically distinct but genetically closely related geographic isolates. Details of specimens as follows; *Menetia surda cresswelli* subsp nov, WAM R131779, an adult male from 12 km WNW Wandina Homestead, photographed by B Maryan; *M. surda surda*, WAMR132655, an adult male from Burrup Peninsula, photographed by B Maryan

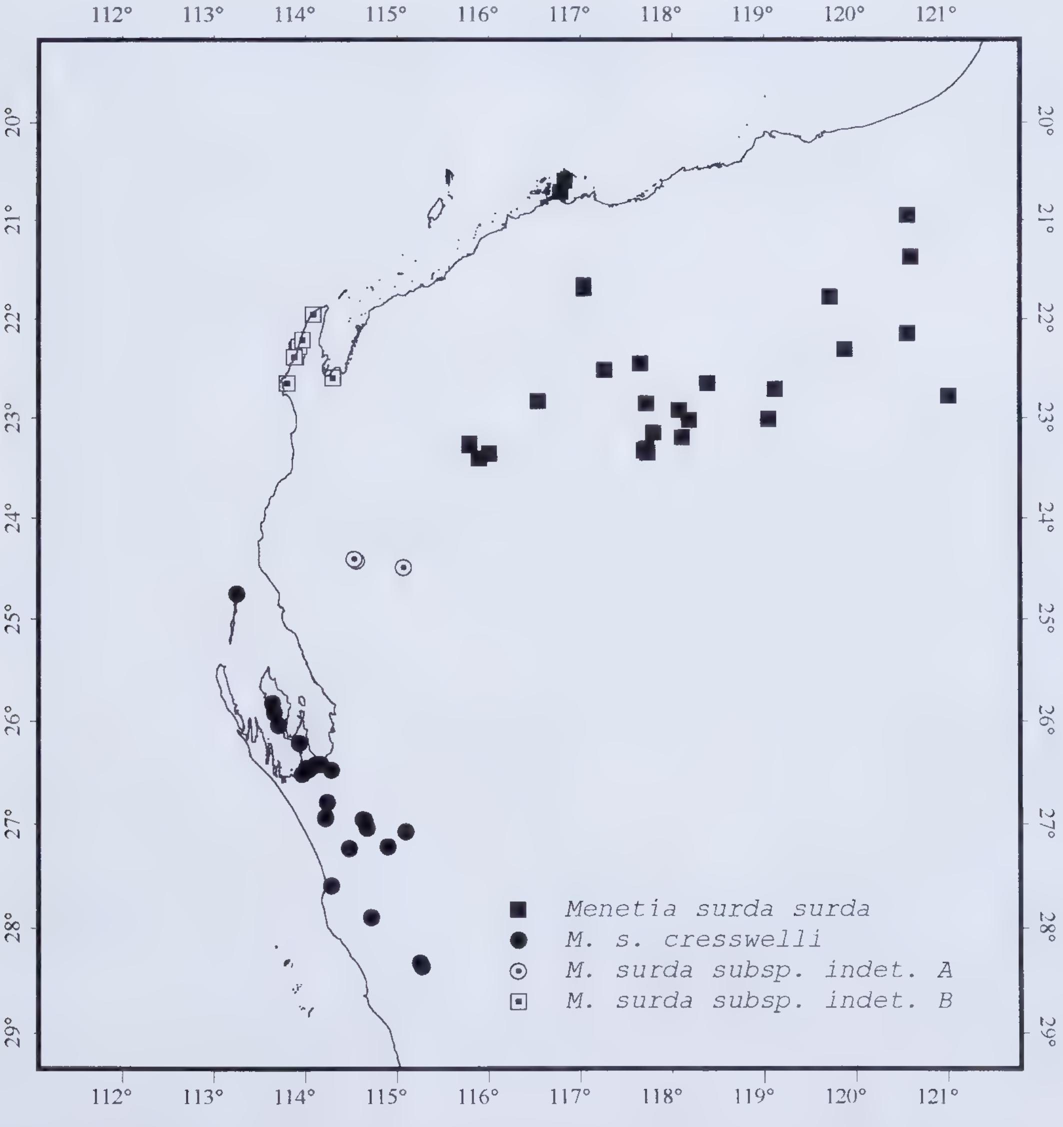


Figure 11. Distribution of the various, morphologically distinct populations of *Menetia surda* in Western Australia. Specimens from the Mardathunna/Kennedy Range area and from Cape Range Peninsula are regarded as *M. surda* subsp *incertae sedis* pending further field survey and analysis.

(26° 32′ 47″ S, 113° 57′ 49″ E): 121087, 121089, 122454; 18 km NW Coburn HS (26° 33′ S, 114° 13′ E): 96546; Nanga (26° 35′ 32″ S, 113° 53′ 22″ E): 127243; **NA5**, 35 km SW Hamelin HS (26° 35′ 34″ S, 113° 53′ 23″ E): 122474-76, 122508, 122523, 125506; 15 km WNW Cooloomia HS (26° 52′ 30″ S, 114° 09″ E): 66340, 66351, 66373; 17 km SW Cooloomia HS (27° 01′ 30″ S, 114° 09′ 00″ E): 66377; 17.5 km SW Cooloomia HS (27° 02′ S, 114° 09′ E): 66353; **NE1**, 12 km NNW Nerren Nerren HS (27° 02′ 50″ S, 114° 34′ 23″ E): 120892; **NE2**, 9 km NNW Nerren Nerren HS (27° 03′ 24″ S, 114° 35′ 21″ E): 121315, 122981; **ZU1**, near Zuytdorp Cliffs (27° 15′ 42″ S, 114° 09′ 11″ E): 123545, 123598); 30 km SE Nerren Nerren HS (27° 19′ S, 114° 51′ E): 60638; 31 km SW Nerren Nerren HS (27° 20′ S, 114° 25′ E): 64327; 1 km SW Nerren Nerren HS (27° 20′ S, 114° 37′ E): 96551; Meanarra Hill, 7 km E Kalbarri (27° 42′ S, 114° 13′ E): 33536; 10 km NW Wandina HS (27° 56′ S, 115° 30′ E): 96678; 12 km WNW Wandina HS (27° 56′ S 115° 32′ E): 131779; 21 km S Galena (28° 01′ S, 114° 40′ E): 71048; East Yuna Nature Reserve, 30 km ESE Yuna (28° 28′ S, 115° 13′ E): 48109, 48112, 48124-25, 48225, 48235-37, 48253, 49927, 75558, 75561-62, 125956-961; Bindoo Hill Reserve, 30 km NNW Tenindewa (28° 30′ S, 115° 14′ E): 48194, 48203.

Diagnosis

A relatively plain *Menetia* with a subdued pattern of 8-10 longitudinal dark lines of subequal strength and spacing. Differs from nominate *M. surda* in having fewer scales along paravertebral series; paravertebral scale series wider than more lateral scales along entire length of body (posterior paravertebrals not widened in *surda*); claws on manus and pes shorter and recurved; lacking conspicuous laterodorsal stripe; and venter with faint longitudinal lines for posterior $^{1}/_{3}$ - $^{2}/_{3}$ of body length (immaculate in *surda*).

Description

A relatively plain *Menetia* with a subdued pattern of longitudinal dark lines. SVL to 30.3 mm; Tail to 52.6 mm; ForelimbL to 7.1 mm; HindlimbL to 10.7 mm. Other mensural and meristic data given in Table 5.

Paravertebral scales 50-60, mean = 55.6 ± 2.2 (sd); scales in 20-24 rows at midbody, modal count 22 (68 % of sample). Paravertebral scales remain wider than scales of more lateral rows along entire length of body.

Plantar surface of manus and pes with bluntly rounded scales. Digits slender, relatively elongate, all terminating in short, recurved claws. Subdigital lamellae with broad ventral calli. SDL 12-17 on manal digit III, modal count 15 (36 % of sample); 21-26 on pedal digit IV, modal count 24 (25 % of sample).

Preanal scales 4, lateral scales overlapping medial.

Nasals divided by posterodorsal cleft; widely separated medially. Prefrontals usually narrowly separated (40 % of sample) or in narrow medial contact (31 %); occasionally more widely separated (19 %) or in broad contact (10 %). Frontal small, shield-shaped, in point contact with frontoparietal. Loreals 2, subequal or anterior higher than posterior. Supralabials 6, 3 of these forming discrete preorbital series. First supralabial usually shorter than second or third. Posterior part of third supralabial wedged below anterior end of fourth. Postsupralabials 2. Infralabials 6. Supraoculars 3, first very large, in narrow contact with prefrontal, abutting supraciliaries 1-3. Second supraocular less than one half size of first, wider than third, abutting supraciliaries 3-4. Supraciliaries 4, first in broad contact with first supraocular; second largest, posterior end wedged between third supraciliary and enlarged ciliary; third more than twice size of fourth. One specimen (R123598) shows unilateral fusion of the first and second supracilairies. Eyelid forms fixed spectacle, entirely clear. Enlarged ciliary scale on posterodorsal margin of orbit, subequal to or slightly smaller than third supraciliary. Preoculars 2, upper scale very small, lower in series with single presubocular. Presubocular usually slightly smaller than lower preocular [both of these scales identified as presuboculars by Taylor (1935), Rankin (1979) and Storr *et al.* (1981)]. Single postsuboculars above fifth supralabial, in series with pretemporals. Upper pretemporal large, in series with supraoculars, narrowly separated from frontal. Primary temporals 2, lower larger than upper. Secondary temporals 2, upper much larger than lower. Frontoparietals fused into large shield. Interparietal distinct with centrally placed parietal eye. Parietals in contact behind interparietal. Nuchals usually in single pair, in lateral contact with upper secondary temporal.

Mental succeeded by large postmental and four pairs of chin-shields; first pair only in medial contact.

Ear aperture concealed by enlarged post-temporal scales [tympanum is not absent, as implied by Storr (1976)], at best a very faint groove to indicate position.

Ground colour of dorsum generally a drab brown, fading to pale grey on flanks; occasionally a darker brown (*e.g.* R123678-9) to almost black (R123545). Head concolorous with body. Dorsum and flanks with total of 8 distinct longitudinal black stripes on each side, running

Table 5

Mensural and meristic data for various subspecies and populations of ***Menetia surda.*** All values are mean ± standard deviation, followed by range and sample size. The two subspecifically unallocated populations are CRP - Cape Range Peninsula and MR/KE - Mardathunna / Kennedy Range. Values are mean ± standard error with range and sample size (n).

	M. surda surda	*M. s. cresswelli* subsp nov	*M. surda* subsp CRP	*M. surda* subsp MR/KE
SVL	26.94 ± 2.97 19.7-32.6 (n = 33)	26.00 ± 3.21 14.6-30.3 (n = 64)	25.14 ± 1.87 21.3-27.5 (n = 19)	31.87 ± 0.69 31.1-32.4 (n = 3)
ForelimbL	6.24 ± 0.66 4.5-7.4 (n = 33)	6.16 ± 0.63 4.4-7.1 (n = 64)	5.91 ± 0.40 5.1-6.6 (n = 21)	6.97 ± 0.38 6.7-7.4 (n = 3)
HindlimbL	8.91 ± 0.90 6.9 - 10.6 (n = 33)	9.19 ± 1.04 5.1-10.7 (n = 64)	8.55 ± 0.48 7.8-9.5 (n = 21)	10.23 ± 0.23 10.1-10.5 (n = 3)
PV	57.81 ± 1.97 50-60 (n = 31)	55.57 ± 2.19 50-60 (n = 61)	55.50 ± 2.70 51-60 (n = 20)	57.67 ± 2.08 56-60 (n = 3)
SDL-M3	14.63 ± 1.01 13-16 (n = 27)	15.14 ± 1.01 12-17 (n = 57)	15.63 ± 1.07 14-17 (n = 19)	14.67 ± 0.58 14-15 (n = 3)
SDL-P4	23.45 ± 1.46 21-26 (n = 31)	23.42 ± 1.69 20-26 (n = 59)	24.16 ± 1.30 21-26 (n = 19)	23.67 ± 2.08 22-26 (n = 3)

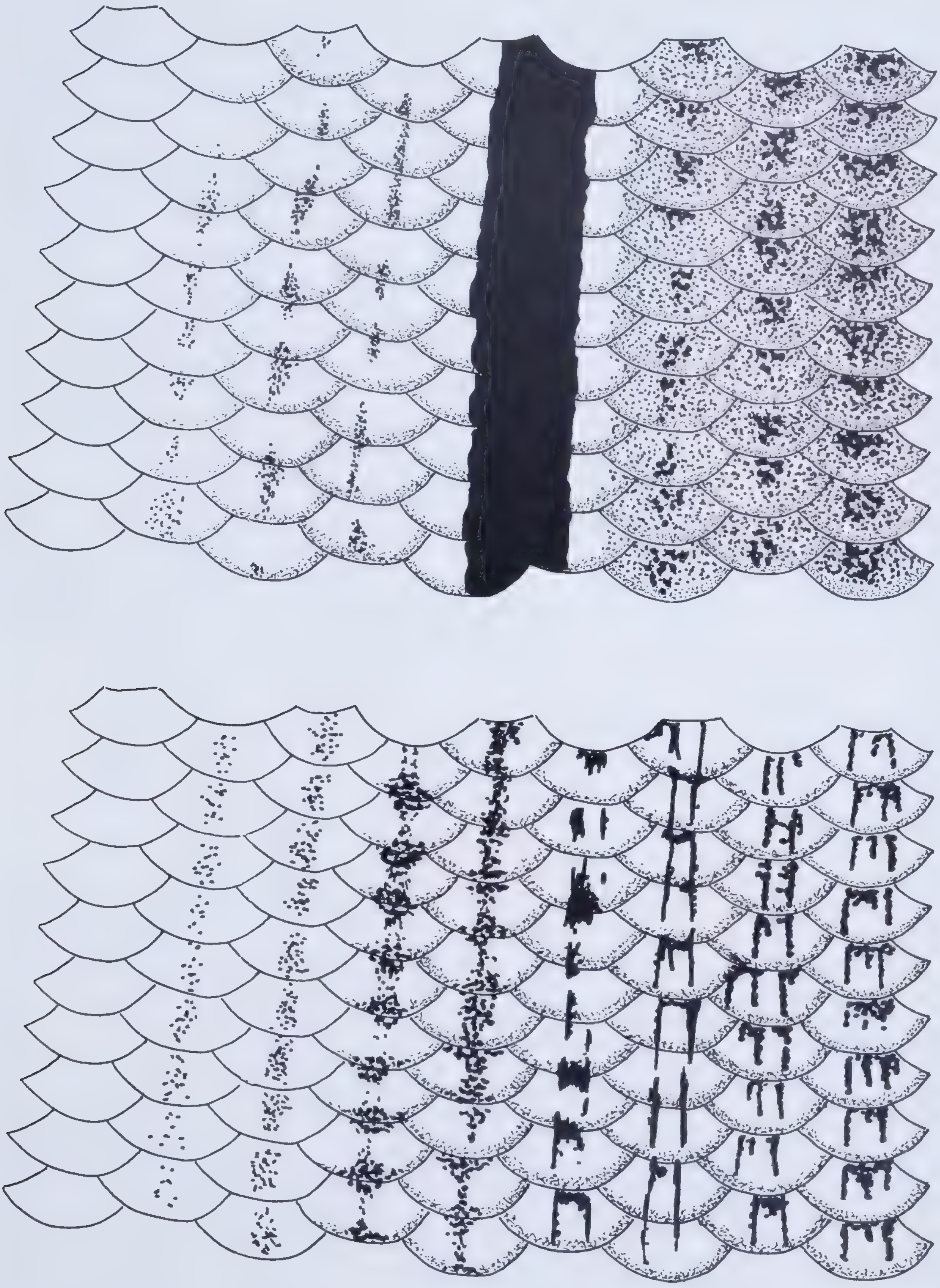


Figure 12. Semi-schematic diagram of the dorsal and lateral body pattern of *M. surda surda* (top; WAM R69777) and *M. s. cresswelli*. subsp nov (bottom; WAM R121089). The pattern is illustrated relative to the boundaries of longitudinal scale rows. The right hand margin corresponds with the dorsal midline.

Table 6

Allozyme profiles of *M. surda surda*, *M. surda cresswelli* subsp nov and two individuals of uncertain subspecific identity (MR) at 20 variable loci. Code for Carnarvon Basin survey sites: MR = Mardathuna , NA – Nanga, NE = Nerren Nerren, PE = Peron Peninsula. Other abbreviations for locality: RH = road-house; NR = Nature Reserve. A dash indicates that the genotype was not assignable at this locus due to poor activity. (The ' EBU-' prefix for Number refers to the accession number for the S.A. Museum's frozen tissue collection).

Specimen Number	Locality	*Acon2*	*Acyc*	*Adh*	*Ak*	*Dia*	*Est1*	*Est2*	*Fdp*	*G6pd*	*Gapd*	*Gda*	*Got1*	*Gpi*	*Me1*	*Me2*	*Mpi*	*PepB*	*6Pgd*	*Pgm1*	*Sordh*
M. s. surda																					
R120031	Hope Downs	a	b	a	b	ce	a	ab	ab	ac	-	b	a	b	b	b	ab	-	b	c	-
R119911	Mt Brockman	a	b	a	b	ac	ab	ab	a	ac	a	b	a	ab	b	b	a	ab	b	ac	c
EBU-S30	Millstream	ac	b	a	b	c	a	ac	ab	c	a	b	a	a	b	-	a	b	-	cd	bc
M s. cresswelli																					
R122981	NE2	b	a	a	b	c	a	a	a	ab	a	b	a	a	b	b	a	bc	ab	cd	b
R121087	NA4	a	b	a	b	c	a	ab	a	a	a	ab	ab	a	b	b	a	ab	b	c	b
R122454	NA4	a	b	a	b	c	a	a	b	a	a	b	a	a	b	b	a	ab	b	c	b
R122523	NA5	ac	b	ab	b	c	a	a	b	a	a	b	a	a	ab	b	a	ab	b	c	b
R123678	PE5	ac	b	a	b	-	a	a	ab	a	a	b	a	a	b	b	a	ab	b	c	b
R36263	Billabong RH	a	b	a	b	cd	a	ab	b	a	ab	b	a	a	b	b	a	ab	b	c	b
R125956	East Yuna NR	a	b	b	b	c	a	b	ab	a	a	a	a	a	b	ab	a	b	bc	c	b
R125961	East Yuna NR	a	ab	a	ab	c	a	a	ab	a	a	ab	a	a	b	b	a	b	b	bc	b
M . s. subsp?																					
R120680	MR3	ac	b	a	b	c	a	a	ab	a	a	a	a	a	b	b	a	ab	b	c	b
R120724	MR4	a	b	a	b	bc	a	a	a	ab	a	a	a	a	b	b	a	a	b	c	ab

through centre of each of SR-1 to SR-8 (Fig 12). Stripes narrow but distinct against pale flanks, becoming wider but less distinct against darker dorsum. All stripes continue forward onto head and neck. Dorsolateral stripe positioned on SR-4; becoming noticably thicker and darker anterior of axilla, extending to posterior margin of eye and continued forward by thin subocular emargination. Distinct loreal stripe extends forward through nostril. Dorsum of head flecked with black. Upper lips barred, continued onto infralabials. Longitudinal lines present but not obvious on very dark individuals (*e.g.* R123545, R123598; both from Zuytdorp cliffs).

Undersurface of throat and anterior part of venter generally immaculate. Posterior $^1/_2$ to $^2/_3$ of venter with very faint longitudinal lines, continuing series of dorsum and flank. Tail with complete series of longitudinal lines. Two specimens from Zuytdorp Cliffs (as above) with venter diffusely pigmented to neck.

Limbs with longitudinal series of dark-brown spots, giving lined appearance. Upper surface of manus and pes spotted.

Details of Holotype

SVL 25.7 mm; Tail 43.5; ForelimbL 5.9 mm; HindlimbL 9.0 mm; paravertebral scales 54; midbody scale rows 22; subdigital lamellae manus III 15; subdigital lamellae pes IV 22; prefrontal scales narrowly separated; ear aperture entirely indistinct; nuchals 1 pair. Adult male with turgid testis and prominent efferent duct.

Etymology

Named for Mr Ian Creswell, formerly of the National Reserve Systems Cooperative Unit, Environment Australia, for his role in facilitating the Carnarvon-northern Irwin Biological Survey, and in particular for his support of systematic studies as a fundamental component of regional biological assessment.

Distribution and variation

The Shark Bay region of Western Australia including Peron Peninsula and Bernier Island, south to Bindoo Hill and East Yuna Nature Reserves, inland of Geraldton (Fig 11). With the exception of the Zuytdorp Cliffs specimens, all southern records are from inland localities although this may reflect access to the relevant sections of the coast. The nearest records of *M. surda surda* are from the Barlee Range.

The two specimens from Zuytdorp cliffs are unusually dark, both dorsally and ventrally. These specimens superficially resemble *M. amaura* Storr, an enigmatic taxon long known only from the holotype (Storr 1978), but more recently recognised from numerous coastal localities in the southern Carnarvon Basin (K Aplin, M Adams & M Cowan, unpublished observations). Interestingly enough, one of the Zuytdorp *cresswelli* specimens (R123598) also resembles the holotype of *M. amaura* in showing unilateral fusion of the first and second supraciliaries (this condition is bilateral in the holotype of *M. amaura*, but this appears to be an individual anomaly in a taxon which normally has a supraciliary arrangement like that of *M. greyii* Gray). In all other respects the Zuytdorp specimens resemble *M. surda*, most notably in having distinct presubocular and lower preocular scales, an enlarged ciliary granule and distinct supraciliaries in contact with the frontal. Unfortunately, tissue samples are not available from either of the Zuytdorp specimens, hence the intriguing possibility that these specimens represent hybrids between *M. amaura* and *M. surda* could not be tested genetically.

Another distinctive population of *M. surda* is represented by three specimens obtained on Biological Survey quadrats on Mardathuna and in the Kennedy Range. With SVL of 31.1 - 32.4 mm, these specimens are larger than any *M. s. cresswelli*, and are larger than all but a few individuals of *M. s. surda*. The digits and claws are relatively long as in *M. s. surda*, but the dorsal pattern is more similar to that of *M. s. cresswelli*, consisting of indistinct black longitudinal lines on a dark brown ground colour. This population appears to be isolated from the main distribution of *M. s. cresswelli*, as no member of the group was obtained on any of the ten Biological Survey Quadrats on intervening Woodleigh and Meedo. The nearest records of typical *M. surda* are from the Barlee Range, approximately 200 km to the northeast of the Kennedy Range.

Genetic differentiation

Representative samples from various populations of *Menetia surda* were included in a broader investigation of genetic variation within *Menetia*. The results of this wider study will be presented elsewhere; for the present it need only be mentioned that the various populations of *M. surda* form a discrete clade which appears to be the sister taxon of an *M. greyii* 'complex', which itself consists of some three or four taxa including *M. amaura* and *M. maini* Storr. *Menetia alanae* Rankin and *M. concinna* Sadlier together form a third major clade.

Within *M. surda*, a total of 8 individuals of *cresswelli* from sites in the southern Carnarvon Basin were compared with three individuals of typical *surda* from the Pilbara and two specimens from Mardathuna. These animals were screened at 39 presumptive loci.

The allozyme profiles of all 13 individuals at the 20 loci found to be variable are shown in Table 6. The remaining 19 loci were invariant; *Acon1, Acp, Enol, Fum, Gdh, Glo, Got2, Gpd, Gpx, Idh1, Idh2, Lap, Ldh, Ndpk, Np, Pgam, Pgk, Pgm2* and *Tpi*.

Menetia s. surda and *M. s. cresswelli* show minimal genetic differentiation, with no fixed differences and a Nei D of 0.022. On Nei D, the Mardathuna population appears slightly closer genetically to *M. s. cresswelli* (Nei D = 0.018) than to *M. s. surda* (Nei D = 0.045). A few loci show differences in allele frequency (*e.g. G6pd, Gpi* and *Sordh* between *M. s. surda* and *M. s. cresswelli*; *Acon2, Acyc* and *Gda* between *M. s. cresswelli* and the Mardathuna population), but small sample sizes preclude any statistical analysis. It is possible that with screening of larger samples of these populations, some of these genetic markers may prove to be partly- or near-diagnostic (a common feature of many 'diagnostic' morphological characters). However, no amount of additional screening will change the general picture obtained in this study of low level genetic divergence among the various allopatric populations of *M. surda*. Elsewhere within *Menetia*, levels of genetic differentiation between sympatric species are somewhat higher, involving several fixed differences. However, there is also good evidence of active hybridization between some of the taxa (M Adams, M Hutchinson & K Aplin, unpublished observations).

The one genotyped specimen of *M. s. cresswelli* from Nerren Nerren is unusually divergent, with unique alleles at *Acon2, PepB, 6Pgd* and *Pgm1*. In contrast, the sample of two individuals from East Yuna Nature Reserve, even further to the south, is genetically consistent with the Nanga and Peron samples. The Nerren Nerren specimen is thus most likely individually anomalous.

Comparison with other taxa

Menetia surda cresswelli shares a number of unusual morphological features with nominate *M. surda* and it seems likely that these taxa are monophyletic to the exclusion of other species of *Menetia*. These include a large first supraciliary in contact with the first supraocular, an enlarged upper circumocular granule and a fully concealed ear aperture. Judging from the condition in other genera of skinks, the first of these characters is probably an ancestral state within *Menetia*, but the latter two are very likely derived conditions and the enlarged circumocular granule is uniquely derived within the genus. The results of the wider genetic data likewise support the monophyly of the populations here included within *M. surda*.

The type locality of *Menetia surda* is Budjan Creek, Corunna Downs, in the northeast Pilbara region; the nominate subspecies is here identified with certainty only from the wider Pilbara region (Fig 11 and Appendix 1 for list of material). The distinctive Mardathuna/Kennedy Range population of *M. surda* and another distinctive population from the Cape Range Peninsula are not clearly referrable to either the nominate subspecies or to *M. s. cresswelli* and are treated here as subspecies *incertae sedis*. Basic mensural and meristic data are contrasted in Table 5 for each population of *M. surda*.

Specimens of *M. s. surda* are similar to *M. s. cresswelli* in basic size and body proportions but differ in having a significantly higher mean number of paravertebral scales, narrower posterior paravertebral scales (*i.e.* not substantially broader than the second row scales) and longer, more projecting claws on the hands and feet. The prefrontal scales are in narrow medial contact in 48% of Pilbara region specimens, but have not been observed in broad contact (one specimen from Tom Price, R127711, has a separate, azygous scale). The body pattern of *M. s. surda* is distinctive, with a well-defined, continuous laterodorsal stripe which separates a plain or irregularly-dashed dorsum from the more boldly-patterned flank (Figs 10B, 12). Anterior to the forelimb, the laterodorsal stripe widens through amalgamation with the outer row of dorsal dashes which here forms a more-or-less continuous line. On the flank, the laterodorsal stripe is bordered below by white midlateral and dark-brown lower lateral zones (contrasting with five or six regularly-spaced stripes in *M. s. cresswelli*). The venter in *M. s. surda* is generally immaculate all the way to the cloaca and the undersurface of the tail is usually lightly-dashed rather than strongly lined.

In some individuals of *M. s. surda* the laterodorsal line is solid and well-defined both anteriorly and posteriorly, extending onto the tail, but is divided into two, narrowly separated lines in the mid-body region (Fig 10B). This 'partially divided' laterodorsal line is observed on occasional specimens from throughout the Pilbara (*e.g.* R78569, Tom Price; R84276, R132655 Burrup Peninsula), but it appears to be especially prevalent in the northeast Pilbara ranges. The few available specimens from this area are also slightly larger on average and have somewhat lower paravertebral counts than specimens from elsewhere in the region.

The Cape Range Peninsula population of *M. surda* is similar to *M. s. cresswelli* in being relatively small with low paravertebral counts and relatively short claws. However, the body pattern is more consistent with that of *M. s. surda*, except that the the laterodorsal stripe is usually 'divided' in the midbody region and the ground colour is paler. The posterior paravertebral scales are unwidened (*i.e. surda*-like) in most individuals, but are broader than the second row scales (*i.e. cresswelli*-like) in some individuals (*e.g.* R61070, R95719). The Cape Range population has an unusually high incidence of moderate to broad contact between the prefrontal scales (38%), accentuating the trend for medial contact observed in *M. s. cresswelli*. In some respects, this distinctive population thus combines features of each of *M. s. surda* and *M. s. cresswelli* and is not readily grouped with either one or the other.

As noted above, the Mardathuna/Kennedy Range population of *M. surda* also shares features with both *surda* and *cresswelli*, although on balance it appears closer to the latter. The prefrontal scales are narrowly separated in two of the specimens but meet in point contact in the third.

Habitat and sympatry

Menetia s. cresswelli was obtained from eight of the Biological Survey quadrats and is otherwise broadly distributed in the southern part of the Carnarvon Basin and south to the Geraldton sandplain. On Nanga it was collected from eucalypt and *Acacia* shrublands over spinifex (*Plectrachne drummondii*) and from eucalypt/bowgada scrub. On Nerren Nerren it was obtained from sandplain quadrats with eucalypts, banksias and *Allocasuarina* over *Plectrachne* or low shrubland, but not from sites with a heavier, sandy-loam substrate. On Peron Peninsula, it was once again present in sandplain habitats with *Acacia* over *Plectrachne*. Somewhat anomalously at Zuytdorp, *M. s. cresswelli* was obtained from a near-coastal limestone slope supporting a low heath, but was absent from quadrats further away from the coast (note that these specimens are also morphologically distinctive).

Earlier capture records indicate that *M. s. cresswelli* has most commonly been obtained by burning 'spinifex'. However, it has also been collected from within and below litter beds over sand in various shrubland communities. Storr & Hanlon (1980:370) summarised the habitat of *M. s. cresswelli* in the Zuytdorp hinterland as follows: "Mainly in soft spinifex (*Plectrachne*) and leaf litter on yellow, brown and red sandplains". Pilbara and Cape Range specimens of *M. s. surda* are also generally noted as coming from spinifex tussocks; however in these areas, the substrate is typically hard stony ground or heavy soils.

Menetia s. cresswelli shows broad distributional overlap with various representatives of the *M. greyii* 'complex'. During the Biological Survey it was obtained in sympatry with members of this group on two of the Nanga quadrats (NA2, NA4) and on both Nerren Nerren quadrats (NE1, NE2). On Peron Peninsula (PE2) and at Zuytdorp (ZU1) it was found in sympatry with *M. amaura*. The genetic data provide no indication of hybridization between *M. s. cresswelli* and any member of the *M. greyii* complex (M Adams, M Hutchinson & K Aplin, unpublished observations), but certain morphological features noted above for Zuytdorp specimens hint at possible interspecific interaction (with *M. amaura*?) in this area.

Other remarks

Storr (1976:198) commented on variation in prefrontal scale contact in *M. surda*; "almost as often contiguous as separated" in the north *vs* "always separated" in the south; and he also noted the distinctively 'striate' pattern of southern individuals. However, Storr's 'northern' sample probably included specimens of both *M. s. surda* and *M. s. cresswelli* (*e.g.* Bernier Island) as well as material from the Cape Range Peninsula. His 'southern' sample consisted of specimens here distinguished as *M. s. cresswelli*. As indicated above, the frequency of medial contact between the prefrontals is slightly lower in *cresswelli* than in nominate *surda*; however, in both populations the frequency of medial contact is greater than 40 % with broad contact present in 10 % of individuals of *M. s. cresswelli*.

Storr *et al.* (1981:165) illustrated the geographic range of *M. surda* as most likely continuous from the Pilbara region south to Geraldton. The more extensive collecting undertaken through the region since that time indicates that the geographic distribution of *M. surda* is actually quite disjunct, consisting of separate northern and southern ranges along with several probable isolates on the Cape Range Peninsula and in the central Carnarvon Basin (Mardathuna/Kennedy Range). Each of these regional populations of *M. surda* is morphologically distinctive, with significant differences in overall size, meristic features and body pattern. These differences might conceivably relate to ecological differences associated with the contrasting substrate and vegetation of these environmentally diverse regions.

Menetia surda surda is widely distributed within the Pilbara region but appears to be nowhere especially common. Although the combined Pilbara sample is still not large, there is some indication of intra-regional variation in size, body pattern and meristics, with specimens from the northeast Pilbara appearing particularly distinctive. In contrast, *M. s. cresswelli* appears to be locally abundant in the southern sandplain habitats and shows very little morphological variation across a large geographic area, except possibly in the peripheral Zuytdorp area. As indicated earlier, the Cape Range Peninsula population appears to combines features of each of typical *surda* and *cresswelli*.

The allozyme data demonstrate that the various populations of *M. surda* are genetically very close. This most likely points to a very recent origin of the various isolated populations, either by range fragmentation (vicariance) or by dispersal with rapid local adaptation and morphological differentiation. However, other, more complex scenarios might also warrant consideration, such as the possibility that morphological differentiation within *M. surda* was present prior to the fragmentation of the species range, perhaps in the form of a north-south cline along the coastal hinterland. The morphological intermediacy of the Cape Range population of *M. surda* could be viewed as consistent with this latter scenario, yet caution is urged by the fact that clines are not readily distinguished from zones of secondary contact on the basis of either morphological or allozyme characters (Endler 1977). This and other questions regarding the evolution of *M. surda* must await analysis of more sensitive nuclear and mitochondrial markers.

In our view, the combined morphological and genetic evidence is best expressed taxonomically through recognition of the Shark Bay population as a distinct subspecies within *M. surda*. This makes it clear that *cresswelli* belongs with *M. surda*, yet gives expression to the significant morphological differences between them. Admittedly, by the same argument, each of the Mardathuna/Kennedy Range and Cape Range populations might also warrant subspecific recognition. However, the former population is too poorly represented for statistical analysis of morphology, and the latter might yet prove to be connected via intermediate populations with the main Pilbara populations. Until the distributions and affinities of each of these outlying populations are more firmly established, we suggest that they be listed formally as *Menetia surda* subsp *incertae sedis*.

Discussion

Many of the recent advances in Australian vertebrate systematics have come through the combined application of morphological and genetic methods of investigation. Morphological studies alone can be effective at identifying patterns of variation, but it is often difficult to decide exactly where boundaries should be drawn between species and/or subspecies. Genetic studies, on the other hand, may give a clear indication of interrupted gene flow and a lack of interbreeding in the case of sympatric comparisons, but they are usually carried out on relatively small numbers of individuals derived from large geographic areas. Moreover, genetic studies alone will rarely lead to taxonomic conclusions owing to the lack of genetic data for type specimens or even topotypic specimens.

Each of the new taxa described in this paper was detected initially through careful and systematic study of museum voucher specimens. However, in each case, allozyme electrophoresis played a critical role in the taxonomic process. For each of *Ctenotus maryani* and *Diplodactylus klugei*, the genetic data were essential in the confirmation of specific status. Both taxa are morphologically cryptic and both had been collected on prior occasions but overlooked by highly experienced field collectors and taxonomists. Indeed, were it not for the confirmation provided by the genetic data, the variation observed in sympatry might easily have been dismissed as polymorphism and individual variation.

In the case of *Menetia surda cresswelli*, the senior authors' initial judgement was that the southern populations were very likely specifically distinct from *surda* on account of the extent of morphological divergence within what is generally regarded as a morphologically conservative genus. The genetic data indicated that specific distinction is probably not warranted; subspecific distinction was chosen as an appropriate level of taxonomic discrimination for *cresswelli*.

The common lack of congruence between morphological and genetic levels of divergence has been noted for various groups of vertebrates (Baverstock & Adams 1984; Ohta 1992; Sheldon & Bledscoe 1993; see Omland 1997 for a contrary view). Among the present series of taxa, the two skinks illustrate this very clearly. In morphological terms, *Ctenotus maryani* and *Menetia surda cresswelli* differ from *C. iapetus* and *M. s. surda* in very similar ways, namely slight changes in meristic values and body proportions (limb lengths, claw size) and subtle but noticeable differences in body patterning. Yet the level of genetic differentiation between the related taxa differs by an order of magnitude, *i.e.* Nei D = 0.022-0.045 between *Menetia s. cresswelli* and *M. s. surda*; and Nei D = 0.328 between *Ctenotus maryani* and *C. iapetus*. The level of genetic differentiation between the newly recognised *Diplodactylus klugei* and *D. pulcher* lies between these values at Nei D = 0.258; yet morphologically, the two species are perhaps as close, if not closer, than any other currently recognised sibling pair within the genus *Diplodactlyus*.

Ctenotus maryani and *Diplodactylus klugei* both qualify as 'cryptic' species in the sense that they exhibit only very subtle morphological differences from, and have been previously 'buried' within, other species, namely *C. iapetus* and *D. pulcher*. However, each of these species pairs suggests a quite different evolutionary scenario. The two *Diplodactylus* species are moderately well-differentiated genetically and have broadly overlapping geographic ranges. They may well be true sibling species which have diverged very little from a common ancestral morphology. In contrast, the two *Ctenotus* species are more distant genetically and may not be true siblings (*C. iapetus* is probably more closely related to *C. quattuordecimlineatus*; and *C. maryani* may be closest to *C. zasticus*); yet *C. maryani* and *C. iapetus* are remarkably similar in morphology. In this case, the morphological similarity could either be due to conservatism (*i.e.* both species retaining an ancestral morphology) or to parallelism (*i.e.* both species having independantly evolved the same form), or perhaps to some combination of the two (*e.g.* conservatism of body proportions, parallel evolution of dorsal and flank pattern). *Ctenotus maryani* is undeniably 'cryptic', yet its crypticity is unusual in that it may well owe as much to morphological parallelism as it does to morphological conservatism.

Elsewhere we have individually argued that the recognition of 'cryptic' species should be a high research priority for Australian herpetology (Aplin & How 1993; Donnellan *et al.* 1993). Here we would like to turn that plea around to deliver a cautionary message for conservation biology.

The steady and ongoing recognition of new species of reptiles, mammals and frogs in Australia makes it abundantly clear that we are still a long way short of a full inventory of species-level diversity in these groups. Keogh & Smith (1996:687) recently expressed the view that "Australia is still a virtual frontier of taxonomic research". This statement was made in the context of a traditional morphometric study of a genus of snakes, but is perhaps even more appropriate in the context of genetic assessment of species-level diversity. The number of genera which have been subjected to anything like a comprehensive genetic assessment is extremely low for all major groups. More commonly, genetic data are available for only one part of a complex genus or as pilot data across a selection of the total available species, and for many other genera of vertebrates (birds included here) there is quite simply no information (published or otherwise) on levels of genetic variation, even between currently recognised species.

Given the current spate of regional assessments being conducted in advance of land acquisition and rehabilitation and for general resource management, we believe that it is essential that we objectively re-examine species-level diversity within the Australian vertebrate fauna. As exemplified by the ongoing studies of the Carnarvon Basin herpetofauna, allozyme electrophoresis can provide the necessary objectivity, but it is most effectively applied to the testing of specific hypotheses generated by prior morphological assessment. To implement such an approach for wider-scale regional biodiversity assessment requires an open-minded approach to ecological theory and zoogeography, a willingness to collect the necessary tissue samples for genetic analysis and a carefully structured protocol for the efficient application of both morphological and genetic techniques. Knowledge only rarely ever comes so cheaply.

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Appendix 1

Other material examined

Ctenotus iapetus Storr 1975

18 KM SE Onslow (21°45′S, 115°14′E): 80314; Vlaming Head (21°48′S, 114°06′E): 61422, 61440; 13 KM S North West Cape (21°54′S, 114°08′E): 27887; 26 KM S Urala (22°00′S, 114°53′E): 30324; 2.5 KM N Yardie Creek (22°19′S, 113°49′E): 611363; 21.5 KM N Bullara HS (22°30′S, 114°04′E): 11691; KM NW Bullara HS (22°40′S, 114°01′E): 50290, 51018; 3 KM E Giralia HS (22°41′S, 114°24′E): 60992-3, 60999, 61148; 30 KM E Ningaloo (22°42′S, 113°57′E): 16883; 30 KM E Ningaloo (22°42′S, 114°00′E): 61310; 16 KM W Marrilla HS (22°58′S, 114°16′E): 63692; 1 KM N Minga Bore (23°00′S, 114°15′E): 116920; 32 KM N Warroora (23°12′S, 113°48′E): 21776; 6 KM N Mia Mia HS (23°20′S, 114°26′E): 71353-4; 10 KM SE Gnaraloo (23°39′S, 113°34′E): 81714-15; 3KM SE Gnaraloo (23°45′S, 113°32′E): 76725-76726; 5 KM SE Gnaraloo (23°46′S, 113°32′E): 71745; 17 KM ENE Gnaraloo (23°48′S, 113°41′E): 81693; 5 KM SE Gnaraloo (23°51′S, 113°34′E): 71594; 9 KM NE Cape Cuvier (24°11′S, 113°27′E): 117225; **CU5**, 8 KM NE Cape Cuvier (24°11′35″S, 113°27′19″E): 119867, 121465, 121473, 126850, 126879, 126906; **CU2**,11 KM E Cape Cuvier (24°13′22″S, 113°30′12″E): 119861, 122909; **CU3**, 8 KM E Cape Cuvier (24°13′23″S, 113°29′29″E): 120405,122911; **CU4**, 6 KM E Cape Cuvier (24°13′26″S, 113°27′41″E): 119877, 119879-80, 119883, 119886, 120406, 125279-80, 126877-78, 126880; Quobba (24°24′S, 113°24′E): 60524; **MR5**, 14.7 KM W Mardathuna Homestead (24°24′21″S, 114°26′40″E): 122892; **MR4**, 11.8 KM W Mardathuna Homestead (24°24′26″S, 114°28′24″E): 120375, 120698, 121547, 122748, 122776, 122778, 126756; **MR3**, 7.7 KM W Mardathuna HS (24°25′44″S, 114°29′60″E): 120407, 120716, 120718, 122725-26, 122728, 122734, 122736, 122858-59, 126196, 126801; **MR2**, 5.6 KM W Mardathuna HS (24°26′36″S, 114°30′43″E): 122838-39; **KE1**, 41 KM from Binthalya Homestead (24°29′36″S, 115°01′51″E): 120524, 121334, 12386-87, 123194, 123219, 123280, 123291, 124169, 125168; **KE2**, 38.9 KM from Binthalya Homestead (24°30′04″S, 115°01′03″E): 120515, 123376-78, 126209.

Menetia surda surda Storr 1976

Dolphin Island, Dampier Archipelago (20° 29′ S, 116° 51′ E): 14329-30; Burrup Peninsula (20° 36′ S, 116° 48′ E): 84274-78, 132655; Warrawagine (20° 51′ S, 120° 42′ E): 13248; Ripon Hills (21° 17′ S, 120° 44′ E): 13247; Millstream HS (21° 35′ S, 117° 04′ E): 94620; 1 km SE Millstream HQ (21° 36′ S, 117° 04′ E): 99808; 3 km S Millstream HS (21° 37′ S, 117° 04′ E): 81395; Budjan Creek, Corunna Downs (21° 42′ S, 119° 50′ E): 13249; 5 km ENE Kurrana Well (22° 02′ E, 120° 29′ E): 73950; 2 km W Rove Hills Mine (22° 05′ S, 120° 42′ E): 74086; Between Nullagin and Roy Hill (22° 15′ S, 120° 00′ E): 68365; 17 km S Riotinto Gorge (22° 21′ S 117° 53′ E): 114446; 24 km NNW Tom Price (22° 24′ S, 117° 42′ E): 76569; 3.5 km NE Mt Brockman (22° 28′ S, 117° 18′ E): 119911,119917; Curran Curran Rockhole (22° 32′ S, 121° 56′ E): 42209; 10 km NW Windell (22° 36′ 00″ S, 118° 27′ 35″ E): 102122, 102146; 21 km WSW Marillana HS (22° 40′ S, 119° 13′ E): 71653; Junction Well. Upper Oakover River (22° 44′ S, 121° 10′ E): 42228-29, 42239-40; 25 km ESE Kooline HS (22° 47′ 28″ S, 116° 32′ 46″ E): 116888; 5 km S Mt Tom Price Mine (22° 48′ 40″ S, 117° 46′ 03″ E): 127711; Coppin Pool Turee Creek (22° 53′ S, 118° 08′ E): 69717, 69755, 69810; Hope Downs (22° 58′ 00″ S, 119° 08′ 20′ E): 120031; 1 km N Mt Trevarton (22° 59′ S, 118° 15′ E): 69710; 21 km NE Paraburdoo (23° 07′ S, 117° 51′ E): 83725, 83728-29; O'Brien Creek Tributary of Turee Creek (23° 10′ S, 118° 10′ E): 69810; 9.4 km N Joy Helen Mine (23° 13′ 00″ S, 115° 46′ 30″ E): 102021; 5.4 km N Joy Helen Mine (23° 14′ 15″ S, 115° 46′ 30″ E): 102014; 0.5 km N Joy Helen Mine (23° 14′ 40″ S, 115° 46′ 30″ E): 102007-008; 6 km S Paraburdoo (23° 16′ S, 117° 40′ E): 83723; 14 km SE Paraburdoo (23° 17′ S, 117° 46′ E): 83779; 4 km N Mount Maguire (23° 18′ S, 117° 44′ E): 94859; 4 km ENE Mt Maguire (23° 19′ 30″ S, 117° 47′ 00″ E): 94874; 21 km NW Ullawarra (23° 20′ S, 116° 00′ E): 25263-64; Barlee Range Nature Reserve (23° 22′ 45″ S, 115° 52′ 50″ E): 102369, 102260.

Menetia surda subsp *incertae sedis*

Mardathuna/Kennedy Range population: **MR4**, 11.8 km W Mardathuna HS (24° 24′ 26″ S, 114° 28′ 24″ E): 120724; **MR3**, 7.7 km W Mardathuna HS (24° 25′ 44″ S, 114° 29′ 60″ E): 120680; **KE1**, 41 km from Binthalya HS (24° 29′ 36″ S, 115° 01′ 51″ E): 125895.

Cape Range population: Yardie Creek HS (21° 53′ S, 114° 01′ E): 13192, 27980; 65 km NNE Ningaloo HS (22° 08′ 52″ S, 113° 53′ 36″ E): 95719; 14 km N Yardie Creek HS (22° 13′ S, 113° 51′ E): 61260; 9 km N Yardie Creek HS (22° 15′ S, 113° 50′ E): 61244; Yardie Creek Mouth (22° 20′ S, 113° 48′ E): 61455-61462, 61491; Yardie Creek (22° 20′ S, 113° 49′ E): 27981-83, 61069-71, 61119, 121405; 20 km NW Giralia HS (22° 33′ S, 114° 14′ E): 61233; 3 km E Norwegian Bay, Ningaloo (22° 36′ S, 113° 43′ E): 32030; 50 km S Yardie Creek HS (21° 53′ S, 114° 01′ E).

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The future of the estuaries of south-western Australia

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Introduction

Professor Arthur McComb who preceded me on the occasion of this talk [acceptance of the "Kelvin" Medal of the Royal Society of Western Australia, July 1997] discussed his investigations of nutrient enrichment in the Peel-Harvey estuarine system. I recognise that eutrophication is still the immediate problem for estuarine management in Peel-Harvey, the Swan and a few other estuaries; however the sources of nutrients are now well known and I hope that eutrophication will soon prove to be a short-term problem for management, scientifically at least. My talk addressed some long-term management problems for the estuaries of southwestern Australia in the context of their history; their Holocene history and their history since 1829. It is a subject that has been rumbling round in my head since 1970 when I spoke about the history of the estuaries at an EPA seminar and Bruce Hamilton asked "How does this help us to manage the estuaries?" I had no answer then and am not sure what *practical* suggestions I can make now.

It is reasonable to assume that the future is likely to be a continuation of the past but only until something happens to change the rules. That is just what happened here with the arrival of "civilised" people whose traditional attitude to the environment was the Old Testament injunction to Noah: be ye fruitful, and multiply; bring forth abundantly in the earth, and multiply therein (Genesis 9-7) [King James version of 1611]. The estuaries of 1997 are no longer the estuaries that European settlers found in 1829, let alone the estuaries where Aborigines fished only 6000 years ago.

Holocene History

All estuaries have been greatly changed by natural processes since they were flooded by the world-wide post-glacial rise in sea level about 6500 years ago, many of them much more than have ours in Western Australia. At that time the estuaries of the south west were 'textbook' estuaries where river water and sea water mixed tidally within the coastline; there was a salinity gradient up their length, and they had a diverse marine-estuarine benthic fauna. By about 3500 BP, catchment sediment had narrowed the riverine reaches, built river deltas, and shallowed the lagoon basins, and longshore drift of coastal sand had built the bars and flood-tide deltas that obstruct tidal exchange to the estuaries today.

The Swan-Canning, Peel-Harvey, Leschenault, Hardy and Nornalup Inlets, and Oyster Harbour are still open to the sea and tidal all the time (Fig 1). Physically they are permanently open (PO) estuaries, but hydrologically they are seasonal, river-flow-dominated estuaries with almost stagnant marine salinity water (36 ppt) for half the year, then are flushed with fresh (< 3 ppt) river water for the other half year (Fig 2). Ecologically, these long-term salinity extremes restrict the diversity of the benthic biota to the few euryhaline species that now flourish in them.

The Holocene transformation of estuaries resulted from a unique complex of physical features (Fig 3):

- sea level was initially at least 1 m higher than its present level;
- the estuaries were already enclosed by coastal barrier dunes (most lithified), with narrow entrances;
- the entrances were sheltered from the prevailing SW winds and swell by headlands or reefs;
- the astronomic tides are microtidal (0.5 m MHHW—MLLW); and
- river flow is highly seasonal (the climate is of Mediterranean-type).

Bar formation is a battle between river flow and the ocean process of littoral drift, and most of the 50 estuaries of the south west are now intermittent estuaries where the bars close periodically;

- seasonally — seasonally open closed estuaries (SO);
- for 3 to 5 years — normally closed estuaries (NC); or
- now permanently — permanently closed coastal lagoons (PC);

and the hydrological extremes are greater than in PO estuaries and the biota are less diverse, especially in NC and PC estuaries. Most purely riverine estuaries are SO.

This series of permanently open to permanently closed estuaries appears to be a natural sequence related principally to differences in the volume and pattern of river flow (see below). River flow to PO and SO lagoonal estuaries comes mainly from the high rainfall area (> 700 mm pa) of the south west where it is large and relatively reliable (except the Murchison River); the catchments of NC and PC estuaries receive < 700 mm mean annual rainfall and river flow is episodic. But the sequence is also related to differences in a) the degree of shelter to the entrances from the SW winds sand swell, b) the

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[†] Ernest Hodgkin passed away on September 23, 1998. This manuscript is published as received, except for minor editing.
P Withers, Honorary Editor

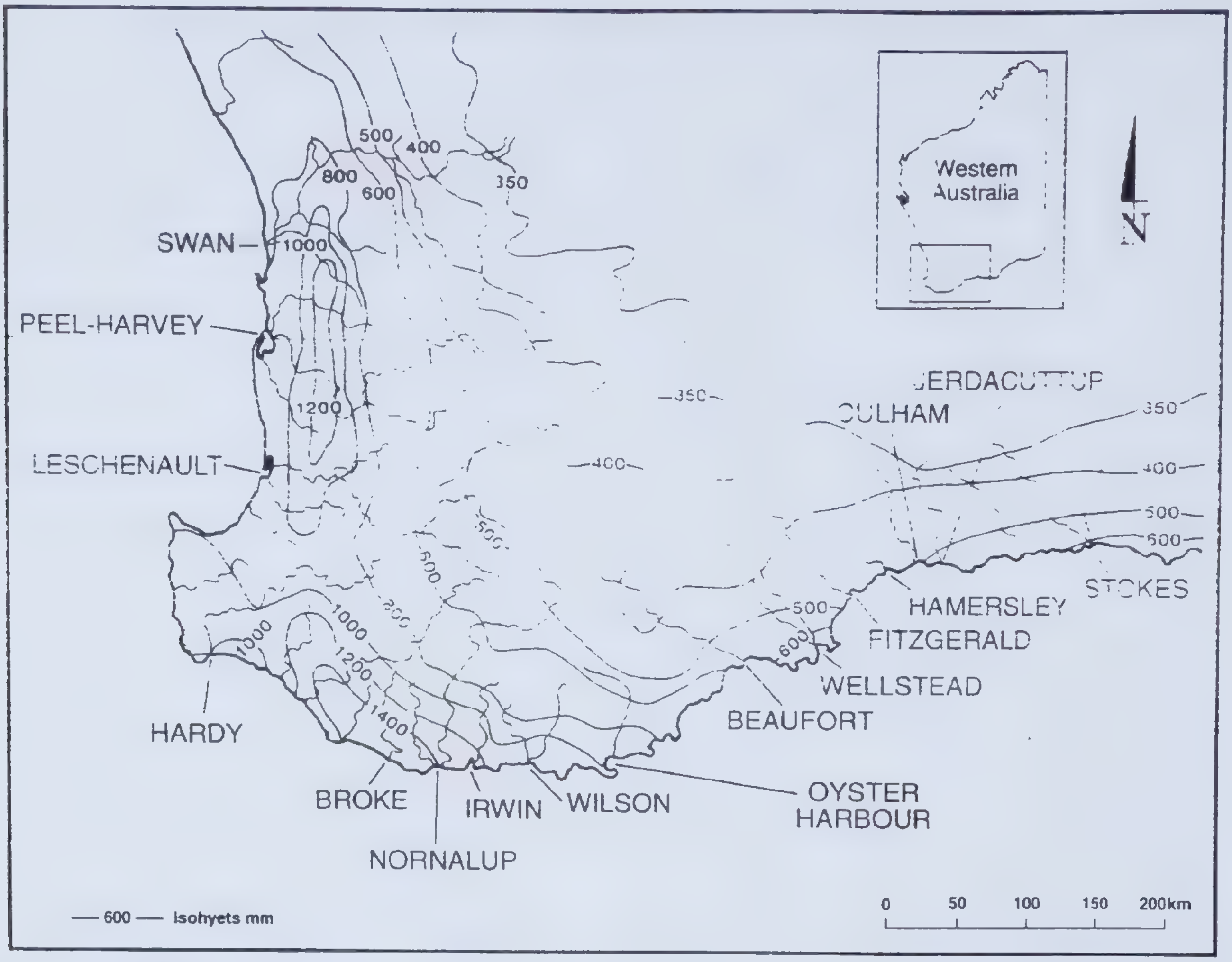

Figure 1. The principal estuaries of south-western Australia.

volume of flood flow relative to the available volume in the estuaries, and c) the volume of catchment sediment transported to the estuaries.

The Holocene history of the estuarine ecosystems of the south west is the subject of a paper by Hodgkin & Hesp (1998).

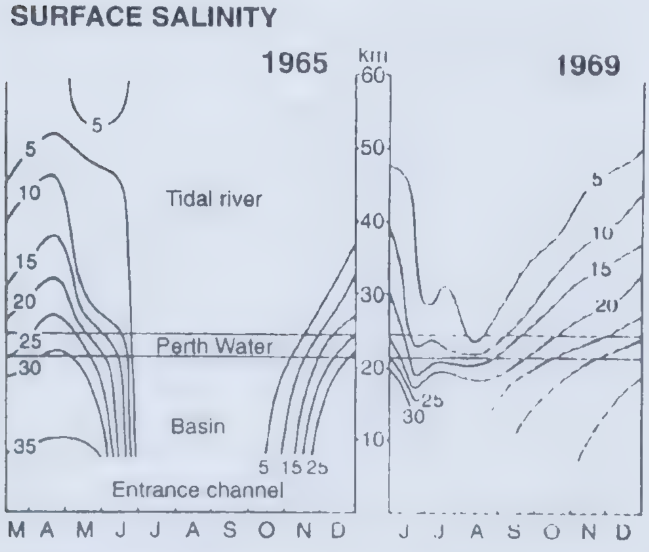

Figure 2. Surface salinity in the Swan Estuary.

1827 to 1997

In 1827 Captain Stirling's crew had to push their boats over the reef at the mouth of the Swan River, along a narrow channel through the flood-tide delta, and drag them through mud laced with fossil oyster shells in Perth Water. They then sailed the 35 km to Ellen Brook, where recently we had to drag our flat bottomed dinghy over sand bars for the last 5 km.

Last century, Perth's sewage poured into the Swan River via Claise Brook; this cannot have done much good for this seasonal estuary. But when C Y O'Connor constructed Fremantle Harbour in the 1890's, he not only greatly increased the tide range in the estuary from < 20% of the ocean tide to now 80% in Perth water, but also increased tidal exchange and tidal flushing of pollutants from the estuary and made it hydrologically a more marine environment .

Peel-Harvey is now a permanently open estuary, but until 1958 the Mandurah bar occasionally closed to water flow. For example, in May 1915, "the water was 20 inches below zero... very discoloured and there is a disagreeable smell along the western portion waters edge caused by stagnation and all floating matter is carried onto this shore by the prevailing winds" (Fisheries and Wildlife Department files). The Dawesville Channel has increased the tide range in the Harvey Inlet from 8% to 63% of the ocean tide, and in Peel from 12% to 45%; it

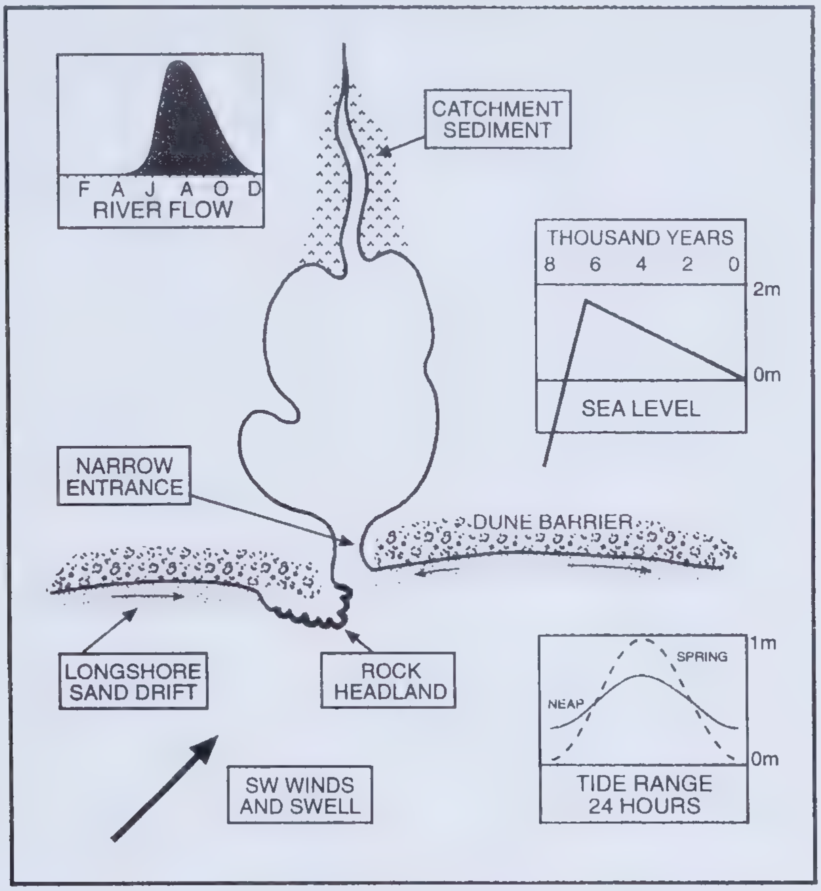

Figure 3. Environmental factors which have combined to transform lagoonal estuaries of south-western Australia during the Holocene.

has greatly improved tidal exchange and flushing and decreased mean residence time from 50 days to 17 days in the Harvey and from 30 days to 10 days in the Peel Inlet (Hart 1995). Bradby (1997) gives a fascinating story of the 'algal problem' in Peel-Harvey and the social and environmental history of the catchment, but it is still too soon to say what changes there have been to the ecology of the estuary.

It was probably not O'Connor's intention to increase tidal exchange in the Swan, and it was only to Bruce Hamilton I dared say in 1970 that if the 130 km^2 Peel-Harvey Estuary was to accommodate the rapidly increasing urban population around its shores and be a healthy estuary again, then it had to have a second channel to the sea. The Swan Estuary is now better flushed than it was last century and the Peel-Harvey Inlet is no longer on the road to being a seasonally closed estuary. I believe that the reversal of the natural process of bar building has made both estuaries now more ecologically sustainable environments.

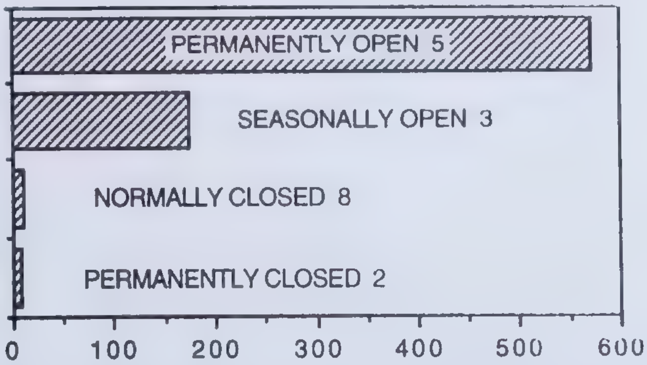

Figure 4. Mean river flow (x10^6 m^3 pa) to the different kinds and number of estuaries.

Sedimentation

All estuaries are 'sediment traps' and are continually being filled with sediment, although that seems to have been a much slower process in our south west estuaries than in estuaries on the NSW coast where sediment has filled estuarine lagoons and left riverine channels winding through their deltas to the sea (Roy 1984). Nevertheless sedimentation is now probably the principal long-term process threatening our estuaries and their tributary rivers.

River flow now averages 570 M m^3 pa to the permanently open estuaries and 170 M m^3 pa to the seasonally open estuaries of the high rainall area (Fig 4). Most of the increased bed load from their low rainfall, now cleared, upper catchments is probably still in the river beds and has yet to reach the estuaries. However the suspended particulate matter is a nutrient-rich organic mud that drops out in the estuaries (and may be resuspended and go out to sea). It has enriched the estuarine ecosystems naturally, but with the application of artificial fertilizers to the catchments it has caused hyper-eutrophication. Within the lagoons, wave action resuspends marginal sediment and reshapes the contours, a slow natural process which extends the shallows that are probably the most productive areas. Several estuaries are being segmented in this way *e.g.* Harvey and Broke Inlets.

Normally closed estuaries of the low rainfall areas (< 700 mm pa) present a very different picture. Mean river flow is small (< 15 M m^3 pa), the bars break from flood flow once in every three to five years, and only remain open briefly. Sediment has already filled most of them almost to sea level. Some always hold water and are productive until the water becomes too hypersaline (*ca* 75 ppt) and the fish die (Beaufort, Wellstead and Stokes Inlets), but others dry up periodically (Gordon, Fitzgerald, Dempster and Hamersley Inlets). What is the long-term future for these normally closed estuaries? What should/can be done about them? Their future looked bleak even before there was clearing in their catchments and now appears to depend on the above environmental factors; degree of shelter to the entrances, volume of the estuaries relative to the volume of flood flow, volume and pattern of river flow, and the volume of catchment sediment transported to them.

There is probably little we can now do about the Beaufort and Wellstead Estuaries, but both the volume of river flow and the volume of catchment sediment to many estuaries have increased dramatically in proportion to the area cleared in the catchments. Clearing is estimated to have increased river flow to the Beaufort Estuary by more than ten times (Surface Water Branch, Water and Rivers Commission, unpublished data). That may have made the bars break more frequently, but not often enough to prevent the lagoons becoming hypersaline, and other estuaries drying up.

Clearing has increased sediment loss from the catchments, although there are few hard data on the rate of sedimentation in the estuaries. The Stokes catchment was cleared in the 1960s and 50-60 cm of wet sediment (20-25 cm dry) had settled in it in the 30 years to 1987; this is probably ten times the natural rate of sedimentation. The 1982 flood was estimated to have taken 100,000 m^3 of sediment from the Pallinup River to Beaufort Estuary. Such sedimentation rates foretell a rapid decline for these estuaries.

The now permanently closed estuaries (Culham and Jerdacuttup) are probably a lost cause as estuaries, but they could continue to be productive coastal lagoons were it not for human activities, as illustrated by the recent history of Culham (Hodgkin 1998).

Management

Each estuary presents its own complex of management problems and decisions must be made in the historical context both of the long term natural processes that have slowly transformed them, and also in the context of the short term effects of human interference on them, and unfortunately in the context of conflicting social and economic pressures. So when were any of our estuaries last 'natural' ecosystems; was it in 1829, or 3000 years or 6500 years ago; and what should their future be? The decision to make the Dawesville Channel was made to reduce the load of plant nutrients in the Peel-Harvey Inlet by increasing tidal exchange to pre-1829 levels in a judgement that did not conflict with what we thought to have been the physical condition of the estuary at that time. However, the Swan-Canning estuary has been so greatly changed by Perth's burgeoning human population that its previous history is now largely irrelevant to management.

The three seasonally closed estuaries, Broke, Irwin and Wilson Inlets, present different management problems related principally to differences in volume of river flow, area of water, nutrient input and human demands on them.

As yet the normally closed Wellstead Estuary (sic) has been little affected by human activities, but the bar only breaks infrequently following episodic river flow from the low rainfall catchment; between breaks, evaporation lowers the water level to expose weed and mud, and the water becomes hypersaline. The residents of Bremer Bay town want to salvage their lovely estuary, although of course it hasn't really been an open estuary for about 3000 years. The easy answer is to "keep the bar open", but that could only be achieved at enormous cost because coastal sand drift fills channels almost as fast as bulldozers can dredge them.

Conclusions

In recent years more consideration has been given to the welfare of the estuarine ecosystems of south-western Western Australia than in the past, but too often political and economic pressures still seem to be the primary considerations on which management decisions are made. The long-term future of these estuaries, and of the river systems of which they are a part, now lies largely with catchment management. What effect has catchment clearing had on them and in particular on sediment transport? Much can be learnt from the sediment record, both about the long-term and the short-term history of the rivers and estuaries. Sediments encode estuarine history and it only awaits decoding from sediment cores taken in the estuaries and on their floodplains to decipher both the Holocene and recent history of the estuaries.

The main message I would like to leave here is: please look beyond the problem of eutrophication when deciding how to manage these estuarine ecosystems and see the primary consideration for decision making as their future welfare.

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Obituary: Ernest Pease Hodgkin

Ernest Pease Hodgkin, otherwise affectionately known as 'EPH' or 'Hodge', died peacefully in his home on September 23rd 1998 after a brief illness. He celebrated his 90th birthday with friends and colleagues on July 26th and the University of Western Australia acknowledged his great contribution to the development of estuarine and marine science in this State by naming the Department of Zoology's marine laboratory at Waterman in his Honour on Friday 18th of September.

Hodge was unique, both as an academic and as a person. He was born in Madagascar, where his parents were Quaker missionaries, and educated in England, taking out his degree in Zoology and Entomology at Manchester University in 1930. He married Mary McKerrow and they went together to Malaya in 1931 where Hodge worked as the Medical Entomologist, studying the habits of mosquitoes that carried malaria in an attempt to combat the spread of the disease. With the advent of the World War II, Mary and their four children were evacuated to Perth in 1941 but Hodge stayed on as a guest of the Japanese in Changi prison for a period of four years. He survived this, while many others did not, by 'keeping busy' in his own words: helping other prisoners less fortunate than himself and turning his hand to repairing the frames of reading glasses with tooth-brush handles! Hodge was always skilful with his hands and few Zoology students realised that many of the benches in the Rottnest Island field station were built by him. After the war he rejoined Mary in Perth and found employment at the University of WA in 1946 as a Lecturer in the Zoology Department. Harry Waring arrived soon after in 1948 and persuaded Hodge to write up his work on the mosquitoes in Malaya as a thesis and he was awarded a DSc in 1950 for a thesis entitled *The Transmission of Malaria in Malaya* which was published by the Institute for Medical Research in Kuala Lumpur as Study No. 27 in 1956. He was later promoted to Reader in Entomology and Vertebrate Morphology and trained generations of zoologists, myself included. He never claimed to be an outstanding lecturer but his heart was always in the subject and we all remember his startling attempts to mimic the flight of insects and his lectures on gastrulation where he attempted to show us how the developing egg involutes at the dorsal lip of the blastopore!

He retired from the University in 1973 and then underwent an astonishing metamorphosis of his own – initiating a whole new research programme on the estuaries of WA for the newly-created Environmental Protection Agency (EPA). His first task was to survey the Blackwood River and Hardy Inlet as there was a proposal to mine the rich mineral sands deposits along the Blackwood and Scott Rivers. This, first, report of the EPA has remained a classic of how environmental studies should be conducted. Although the report recommended against mining, Hodge was always typically modest in saying that the project foundered, not because of his study, but simply because the economics at the time were not favourable. Hodge had always been interested in marine environments and became fascinated by the many estuaries that dot our WA coast. He directed the study on the Peel-Harvey estuary at Mandurah, leading to the construction of the Dawseville cut which has substantially reduced the problem of algal growth. He worked, until the day he died, at trying to understand the geomorphology and evolution of these estuaries and the suite of organisms that inhabit them. His last scientific publications – two appeared only months before he died and one is in this issue – were devoted to this topic. His greatest regret was that he would now not be able to complete the book he had planned to write on WA estuaries, tying the whole story together.

As a young student I worked for Hodge over one summer break and almost didn't survive the experience! He was up at dawn, on the reef all day long, and never bothered to eat or drink unless reminded. He loved camping on the beach and all his skills as a Scout Master came to the fore. Everyone who knew Hodge recognised in him a person of exceptional integrity and honesty, dedicated to the help and betterment of those around him. He never had an unkind word to say – even against his detractors, and there were some – and he carried into his everyday-life his deep-felt religious convictions that flowed from his membership of the Quaker family. He provided students with an example of a deeply-religious person who was neither a zealot nor a weakling. He held strong views and defended them when he needed to, and those who knew him were well aware of how firm he could be at pursuing a goal to its end. To this end he established, just before he died, a trust to foster research on estuaries and continue his life-long work. Those of us who knew Hodge intimately were privileged to have had pass through our lives such an exceptional person, of whom there are so few, and he enriched us all by his being.

**[Don Bradshaw, Head, Department of Zoology,
University of Western Australia]**

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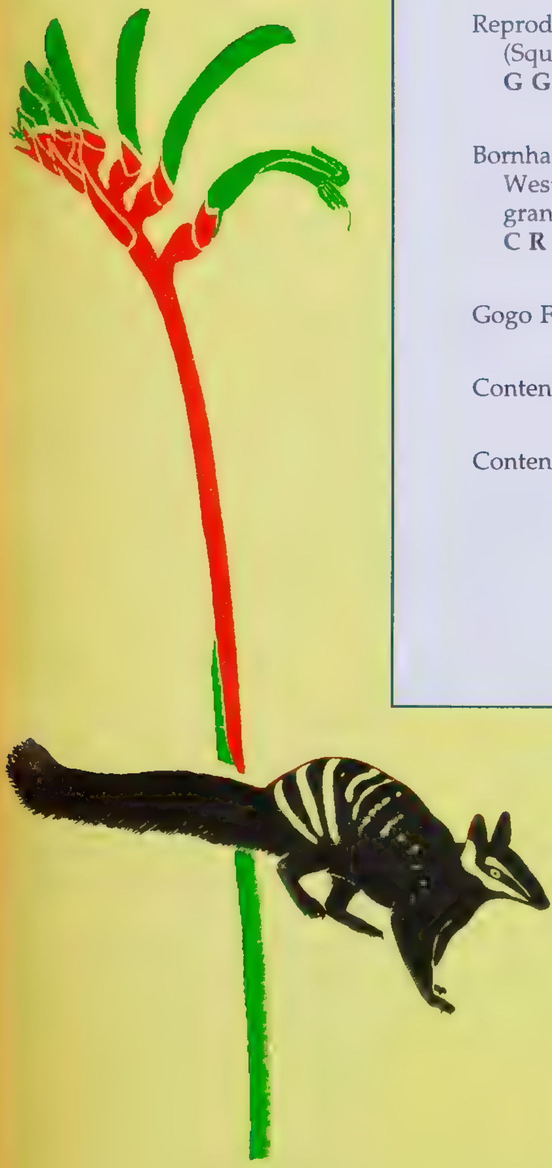

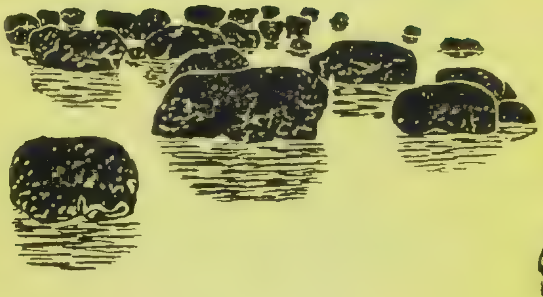

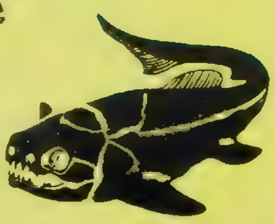

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor), and the Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Review of how indigenous people managed for water in desert regions of Australia

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Abstract

Traditional knowledge, oral instruction and stylised mapping were all important to Australian Aborigines in defining the type of water supplies available in a particular region, and assisting in their location. Observations of birds, especially the more sedentary species such as the zebra finch (*Poephila guttata*), could be significant. Specific sources of water utilized by indigenous people included; flooded gnammas (rock-holes), soakage-wells in permeable sediments, clay dams, flooded claypans, riverine waterholes, mound springs, rain-water accumulated in tree hollows (especially in *Allocasuarina decaisneana*), water from excavated tree roots (especially from mallee eucalypts), dew, and water from the body of the water-holding frog (*Cyclorana platycephala*).

Introduction

The ability of Australian indigenous people to survive in the desert regions where rainfall is low (<200 mm pa), episodic and unreliable, and evaporation is exceptionally high (>3,000 mm pa), has long excited the popular imagination. Most of the early European explorers expressed awe and wonder at the extraordinary ability of Aborigines to survive in what they regarded as hostile if not "impossible" regions. So great was the respect of early explorers for the water-locating ability of Aborigines that several of them (*e.g.* Austin 1856; Calvert 1897; Carnegie 1898; Wells 1899) felt obliged to adopt the extreme and ethically-repugnant measure of depriving Aborigines of their liberty and forcing them to find water. After being deserted by some Aborigines in the Gibson Desert in 1897, Wells (1899) wrote "I then regretted not having chained one of the tribe [a practice adopted by him in December 1896], in spite of my promise to the contrary, for *without a [Black] guide in such country one is almost powerless*". Reading today about incidents such as this serves as a timely reminder that there has been a strong and unfortunate tendency not to give proper recognition to the key importance of Aboriginal knowledge in the exploration and development of Australia (*cf* Reynolds 1990).

One human physiological imperative is an adequate intake of water. Hence the adage "water is life" or, as Giles (1889, v1, p292) put it, "Life for water he [the explorer] will at any moment give, for water cannot be done without". Despite the often meagre nature of water resources, desert Aborigines were, as a rule, able to satisfy this physiological imperative. The purpose of this review is to bring together in convenient form some rather scattered literature (especially in a temporal sense - the references span 145 years!) on how and where Aborigines obtained water in desert regions. Few attempts have been made during the past few decades to review this topic comprehensively, and that of Reim (1962) is in a foreign language. Kavanagh (1984) provided a valuable compilation on "survival water", but his review included some sources (*e.g.* bores) and methods (distillation and those dependent on polyethylene sheets) that were foreign to traditional Aboriginal culture. The opportunity to make first-hand observations to add to the body of knowledge sketched in this review has now gone; the last of the small groups of Aborigines living a strictly traditional life in the desert probably disappeared in the late 1970's - at least there is good evidence that this was the case for the Gibson Desert (Peasley 1983).

General Aspects of Water Location

The role of culture and traditional knowledge

Of key importance to the survival of indigenous people in deserts was the role of oral instruction and stylised mapping of traditional knowledge regarding the type and location of water supplies. Gould (1969) pointed out that the sequence and location of water sources were memorized by Aborigines, and adults would instruct children as groups passed along a chain of waterholes. A knowledge of name sequence and the approximate location of water bodies would often extend beyond the regions that a person had actually visited. Kavanagh (1984, p2-23) also stressed that prior knowledge of the location of surface waters, and the approximate volume contained in them, was of paramount importance for the survival of traditional desert dwellers.

After a period of rainfall, which in Australian desert regions is irregular or episodic, Aborigines would move out to exploit the smaller bodies of water while they still existed. They would forage thoroughly around one of these before moving on to the next. Eventually they would be forced to retreat to the larger and more permanent sources of water. Depending on rainfall, Aborigines would sometimes visit a single reliable waterhole repeatedly within the same year or be compelled to migrate along a chain of water sources to a completely different region without returning to the original site for perhaps two or three years (Gould 1969).

Gould (1984) mentioned the use of smoke signals to indicate that water had been found and to call others to converge on that spot.

Thomson (1962), in a narrative of the Bindibu [=Pintupi] Expedition of 1957, described how he spent several weeks with Aborigines in what is probably the most formidable of all the Australian deserts - the Great Sandy Desert, Western Australia. Just before parting company with these people he was given a very generous gift; a tutorial about their desert waters and a priceless "map" to assist their location. It is worthwhile reproducing Thomson's account of this episode as follows:

> "Just before we left, the old men recited to me the names of more than fifty waters - wells, rockholes and claypans - including those that I have described in this narrative; this, in an area that the early explorers believed to be almost waterless, and where all but a few were, in 1957, still unknown to the white man. And on the eve of our going, Tjappanongo produced spear-throwers, on the backs of which were designs deeply incised, more or less geometric in form. Sometimes with a stick, or with his finger, he would point to each well or rock hole in turn and recite its name, waiting for me to repeat it after him. Each time, the group of old men listened intently and grunted in approval - "Eh!" - or repeated the name again and listened once more. This process continued with the name of each water until they were satisfied with my pronunciation, when they would pass on to the next. *I realized that here was the most important discovery of the expedition - that what Tjappanongo and the old men had shown me was really a map, highly conventionalized, like the works on a "message" or "letter" stick of the Aborigines, of the waters of the vast terrain over which the Bindibu huunted.*" [see Fig 1].

Tindale (1974, p63, fig23) reproduced a comparable "map" of water resources prepared by Katabulka of the Ngatatjara [Ngaatjatjarra] tribe in the Warburton Ranges of Western Australia. This again used spirals to show the location of pools and soakage-wells. The importance of native water maps and associated names in the establishment of the Canning Stock Route was discussed by Tindale (1974, p148).

Seeking help from birds

Magarey (1899), in his review of Aboriginal use of desert waters, stated that, "As thoroughly reliable guides to water in very dry regions the birds have no rivals."

The zebra finch (*Poephlia guttata*), striated pardalote (*Pardalotus striatus*) and red-browed pardalote (*Pardalotus rubricatus*) excel as desert water-finders. The zebra finch is a very sedentary species (the longest movement recorded is only 24 kilometres; Blakers *et al.* 1984) which must have fresh water, so a sighting of it in the desert is very significant. Various pigeons, such as the crested pigeon (*Ocyphaps lophotes*), the forest bronzewing (*Phaps chalcoptera*), and the flock pigeon (*Phaps histrionica*), are also good water "diviners". In addition, Kavanagh (1984) lists both the diamond dove (*Geopelia cuneata*) and the budgerigar (*Melopsittacus undulatus*) for the Simpson and Western Deserts. Wells (1899) described how, in the Great Sandy Desert, his attention was attracted by the noisy flight of a "crested bronze-wing pigeon" which he decided to follow; he was soon rewarded by finding "a splendid native well of a permanent character in sand and soft sandstone".

Specific Sources of Water

Rock-holes (including gnammas); *water lying in hollows on hard, impermeable rock.*

Gnammas are rock-holes (Fig 2) commonly found in outcrops of hard rock, particularly granite, and especially on the top of domed inselbergs (Twidale & Corbin 1963). They are formed over long periods through the gradual enlargement by chemical weathering of what is initially a small cup-sized depression. The word "gnamma" is of Aboriginal origin and comes from the Western Desert languages which were spoken over a huge area of arid country mostly in Western Australia, but also extending into South Australia and Northern Territory. The Western Desert people use this word, or a close phonetic variant of it, to refer to a rock-hole (usually in granite) and especially one likely to contain water. In fact, Tindale (1974) defined a gnamma not as rock-hole, but as a "rockhole *of water*". The word is now firmly established, both in common parlance and in a technical (geological) sense.

One of the earliest written accounts of Australian gnammas (although that term was not used) was that of Austin (1856) who, like several nineteenth century explorers who followed, held an Aborigine captive for the purpose of finding water, during his exploration of the Murchison region of Western Australia. Austin described how his captive led his party to a water-hole in a region where they would never have thought of searching for one, and noted that his party "depended upon the precarious supply of rainwater accumulated *in the hollows of the rocks*".

Giles (1889, v1, p217) provided the following description of what was clearly a gnamma that he encountered in late October 1873:

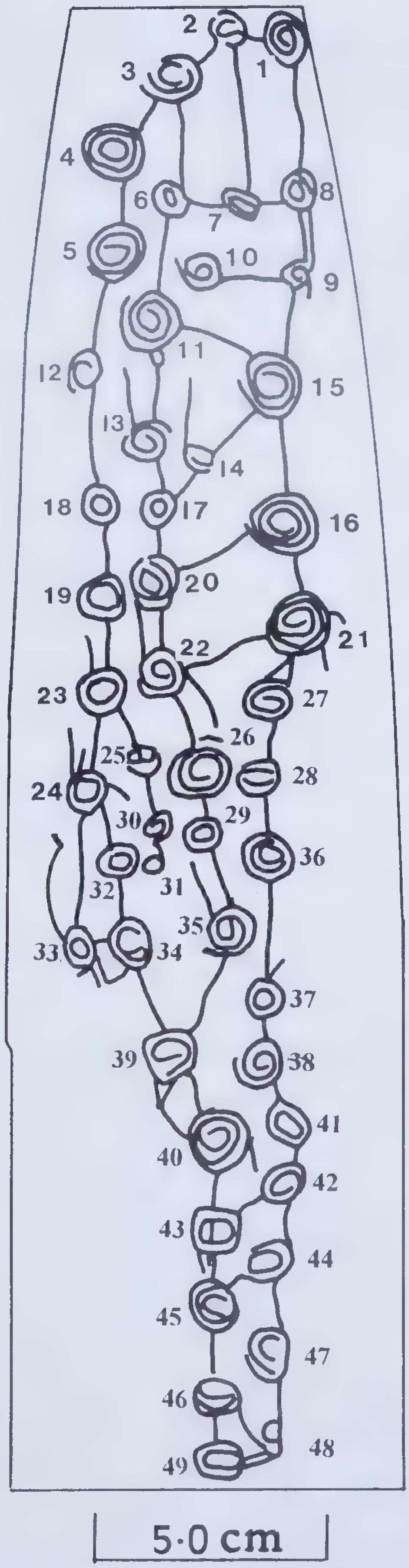
> "Searching about [on a hill of bare rock] we found another of those extraordinary basins, holes or cups washed out of the solid rock . . . . . . From this singular cup we obtained a sufficient supply of that fluid so terribly scarce in this region."

A little earlier, Giles had bestowed the name "The Cups" on a hill (close to Warburton, Western Australia) for its several gnammas. Giles' (1889, v1, p211) account read:

> "Searching about [on a bare rocky hill], I found several small holes or cups worn into the solid rock; and as they mostly contained water, the horses were unpacked, while a further search was made. This hill was always after called the Cups."

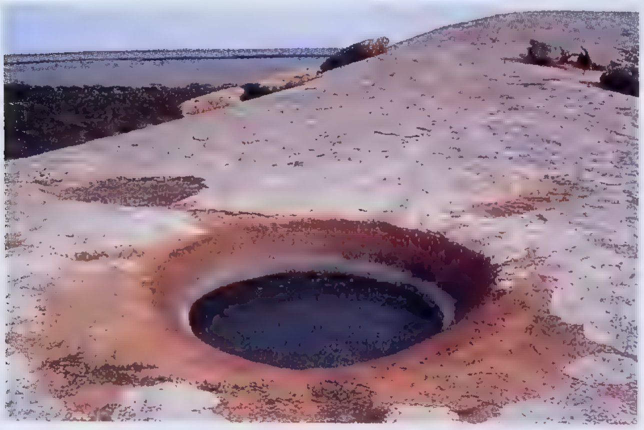
Lindsay's (1893) narrative of the Elder Scientific Exploring Expedition recorded that on 2 October 1891 he was directed to "a fine 'gnamer' rockhole" at Symon's Hill in the vicinity of Fraser Range in Western Australia. Subsequently, Calvert (1897) and Carnegie (1898) used the term "namma-hole." All three authors were referring

1. Labbi-labbi
3. Liuwiringa
5. Maiyada-maiyada
7. Kirindji
9. Markodarindja
11. Wirrkaldjarra
13. Luwano
15. Tjul'tjun'waridji
17. Tildi
19. Kuna
21. Yinindi
23. Tanda
25. Palta
27. Binbiyan
29. Yirabanda
31. Yappadarra
33. Yuldumallo
35. Mukubanda
37. Karruwildji
39. Kiribarro
41. Wangadjarro
43. Tjimarri
45. Wirrarigulong
47. Miltji-miltji
49. Lola



2. Tananga
4. Kunnamannera
6. Wirra-wirra
8. Kanandibaroo
10. Kampanbarro
12. Pinna
14. Kira
16. Dandju
18. Wakilbi
20. Pintinba
22. Yalbirrimanno
24. Kurandal
26. Kura
28. Tjipallalla
30. Dangalli
32. Timbabiddi
34. Kunagarri
36. Mari-mari
38. Wallabarrarba
40. Yanna
42. Wornba
44. Kunananno
46. Danneriyono
48. Papulba

Figure 1. A highly conventionalized map of the Western Australian water resources of the Bindibu [=Pintupi], as carved into the back of a spear-thrower. Redrawn from a photograph of Thomson (1962). The soakage-well known as "Lola" (number 49) is described in a quotation contained in the text of this article.



to a rock depression capable of holding water. In fact, "gnamer rockhole" and "namma-hole" are both tautologies because the Aboriginal word "gnamma" by itself meant a rock-hole.

There can be no doubt that rock-holes (many of which were true gnammas in the sense of my initial definition) were of key importance to Aborigines dwelling in the arid regions of Australia for many thousands of years before white settlement. Indeed, Aboriginal tracks in many regions of Australia were largely governed by the occurrence and distribution of rock-holes. The Aboriginal tracks that radiated out in all directions from Ooldea Soak in South Australia (Johnston 1941; Berndt & Berndt 1942) provide a good example.

It is thought (*e.g.* Jutson 1934) that both animals and Aborigines played a significant role in the enlargement of some gnammas by scratching debris and weakened rock from the bottom and sides while tapping the last vestiges of water. Further, Tindale & Lindsay (1963, p65) pointed out that Aborigines sometimes diverted water into a gnamma by chipping grooves in the surrounding rocky slopes. There are several reports of Aborigines (and later European pioneers) covering gnammas with branches or flat slabs of rock to cut down on evaporation, and to keep out wild animals which not uncommonly fell in and drowned, and thus polluted a precious supply of water. Helms (1896), for example, noted that Aborigines filled rock-holes with loose sticks to prevent animals gaining access to the water. He also described how the Aborigines got very excited when one of his camels micturated on the rock and they quickly placed handfuls of earth in front of the flow of urine to prevent pollution of the water in a gnamma.

Some rock-holes, including many found in sandstone, have been produced by fracturing or some agency other than the slow enlargement of a small concavity by chemical weathering and are therefore not gnammas (see Kavanagh 1984).

Soaks (native wells); *water that seeps into hollows dug in freely permeable sediments.*

Smyth (1878, v2, p245) quoted the explorers Grey and Eyre as praising the ability of Aborigines to dig wells through loose sediments. So called "native wells" or "native soakage-wells" were commonly holes dug into sand or soil lying next to the point where a sloping surface of hard, impermeable rock disappeared beneath a flat plain. The upraised rock surface serves as a rain-water catchment and the run-off soaks into the soft sediments surrounding it. Sometimes the wells were located in swales between sandridges and with no close proximity to rocky outcrops (Rowlands & Rowlands 1965). In such cases there may have been a widespread subsurface water table that was accessible only in the more depressed regions. Generally the depth of these wells did not exceed about 4 or 5 metres, but an average depth was only about 1.5 metres. In the case of deep wells, the sides were secured with pieces of timber and brushwood and cross-pieces were left to serve as a ladder (Basedow 1925, p96).

The word "springs", even when given the apparent authority of incorporation into proper nouns, seems often to have been misapplied to soakage-wells. Jack (1915), for example, noted with respect to the Indulkana Springs in South Australia that "[these] springs may be better described as holes in a saturated sponge of alluvial than as true springs." He also quoted Captain Hubbe's opinion regarding the Oowallinna Springs that, "I am fully convinced that this so-called spring is simply a strong soakage".

Helms (1896) noted that well-holes were often filled with sticks or sand to prevent evaporation and stop animals from drinking or fouling the water. Small soakages under rocks near the base of hills were, after use, always completely covered up again on departure.

Soaks and their importance to travellers were well described by Carnegie (1898) who, however, seemed to make the probably unnecessary assumption that some sort of underground rock basin is a necessary prerequisite for water to flow into an excavation into the soil surrounding a rocky outcrop. While a hidden rock basin or underground rock dam would create a favourable situation, it seems a safe assumption that localised water-tables may become established even where a bedrock surface slopes away continuously beneath the regolith. Wells (1899) reported that "from Mount Bates to the Fitzroy River no surface waters were found in the [Great Sandy] desert, and I am of the opinion that none except native wells are to be found. These are numerous; but *without the assistance of a [Black] guide, or except by running the tracks of natives, they are most difficult to discover.*"

Basedow (1906), who participated in the South Australian Government North-west Expedition of 1903, described the occurrence of several native soakage-wells at the base of granitic hills in the Musgrave Ranges. The same author pointed out that natives sometimes exploited soakage-wells that were located in the sandy beds of superficially dry rivers. Likewise, Strehlow (1947, p60) mentioned that the Western Arrernte Aborigines dug soaks to obtain water anywhere along the bed of the Finke River from Japalpa to Running Waters.

Thomson (1962) made some interesting comments about the extraordinary capacity, based on traditional knowledge and long experience, of Bindibu Aborigines to locate soaks and wells in the desert; in effect they were able to see these features clearly where Europeans would see nothing. Thomson's comments are as follows:

> "There was certainly a great deal more water in the desert than had been assumed by white man, but the location of the wells, soaks and springs on which the Bindibu depend was known only to these people. Most important of all, its behaviour under diverse conditions was familiar to them from life-long experience, backed by traditional information that was handed down from generation to generation by word of mouth. A few days after we went to Labbi-labbi, Hosmer and I went back to the stranded Jeep with some men. They led us to a small well that had a plentiful supply of good water, only a mile from the place where the Jeep was bogged. This was Lola [see Fig. 1], typical of the wells of the remote desert. Wells of this type are less impressive than clay pans and rock holes, certainly the least spectacular of all the desert waters. But in times of drought they are the most dependable. *The difficulty in this country is that there is no way in which the white man can find the wells and soaks, nor, as a rule, is there anything in the lie of the land to explain why the water is there when he does find it.* Lola was situated at the bottom of a depression among low hills and dunes and here, even at an advanced stage in the hot season - well into September - the water-table was only 3 feet from the surface. The well itself was about 14 inches in diameter and there was a step about 2 feet down on the shelving bank. The people had no drinking utensils and when they came to water, each one in turn knelt down and drank, like an animal. Of Lola, the Bindibu say 'nabba pala' - good water."

Gould (1970) described a native soakage-well located at Pulykara, near Mt. Madley, in the centre of the Gibson Desert. This well, which was one of the most dependable sources of water in the region, had been dug down to a depth of about 4.5 metres to reach the water table lying beneath the superficially dry bed of a lake. Likewise, in the western Gibson Desert, the well known as Ngarinarri sustained the aborigines, Warri and Yatungka, the so-called "last of the nomads", during a prolonged drought in the 1970's (Peasley 1983, p87). This well, which was dug through a claypan, was 3.5 metres deep.

Impoundments; *dams constructed from clay with wooden shovels*

Dams of native construction were unusual. However Giles (1889, v2, pp92-3) came across a substantial crescent-shaped clay dam which had been built by Aborigines at Pylebung in western South Australia. The clay had been dug out of a muddy hole with wood shovels to form a dam 18 metres long, 1.5 m thick at the base, 0.6 m across the top and 1.5 m high. Later (Giles 1889, v2, pp170 & 184) this expedition came across a second smaller native clay-dam and found that Aborigines had dug out a "tank" or hollow for water storage purposes at Boundary Dam (named for its location near the border between South Australia and Western Australia).

Murray (1902) described two native dams at Paraminna to the north of Fowler's Bay in South Australia. Here the excavated clay had been reinforced with twigs and branches and formed into a U-shaped dam with a basal width of about 1 metre and a height of about 60 centimetres. Serventy (1961) briefly mentioned Kalgarbin, a dam built by Aborigines in the Great Victoria Desert. Hercus (1990) referred to first-hand accounts of Aborigines in the Simpson Desert prolonging their water supply by building dams across the deeper claypans. When these supplies were exhausted they reverted to soakage-wells.

Claypans; *water lying in a depression in soft sediments with low permeability*

Giles (1889, v1, p39) described a claypan as follows:

> "A clay pan is a small area of ground, whose top soil has been washed or blown away, leaving the hard clay exposed; and upon this surface, one, two, three, or (scarcely) more inches of rain water may remain for some days after rain: the longer it remains the thicker it gets, until at last it dries in cakes which shine like tiles; these at length crumble away, and the clay pan is swept by winds clean and ready for the next shower. In the course of time it becomes enlarged and deepened."

The two salient and rather obvious features of claypans are their ephemerality and high turbidity. They range in size from tens to hundreds of metres across. The shininess of a dried pan referred to by Giles is caused by the extreme fineness of the particles deposited at the final stage of drying (Basedow 1906). The occurrence and Aboriginal use of claypans or "warla" in the Great Sandy Desert was discussed by Lowe & Pike (1990) who pointed out that when they held water they were favoured camping places because they attracted game.

Although sometimes put into a separate category, it is convenient to include with claypans those basins that are called by the Aboriginal word "gilgai". These are small sub-circular depressions 1.5 - 7.5 metres in diameter (Ollier 1966) which, like claypans, have a floor of clay and provided a strictly ephemeral source of water.

Riverine waterholes; *water in holes scoured out of river beds by water movement*

In the low lying regions of central Australia, water-courses scour out coarse bed material during rare floods, and quite large holes may be formed, especially where

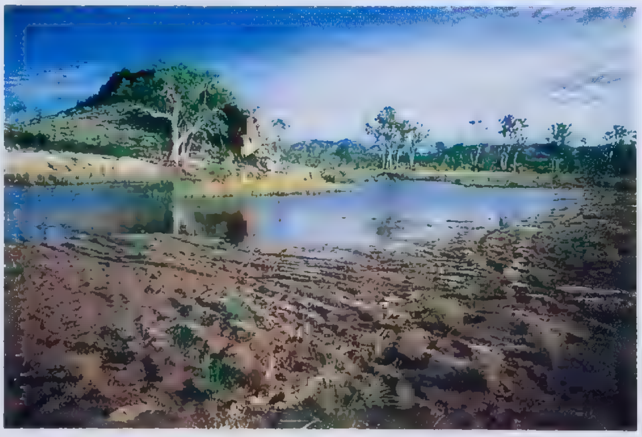


Figure 3. A semi-permanent waterhole located in the bed of the Finke River, near its source, 3 km upstream from Glen Helen Gorge, Northern Territory.

bends occur. After an episodic filling, many of these waterholes suffer rapid losses through evaporation and seepage, and quickly disappear. However, some quasi-permanent waterholes of this kind may occur. Strehlow (1947, p60) mentioned five important "permanent" waterholes frequented by the Western Arrernte Aborigines along the upper reaches of the Finke River (Fig 3), while Mabbutt (1971) pointed to 15 such water bodies along this same river to the south of the James Range. Similar waterholes also form along the Alberga, Lander and Palmer rivers in central Australia (Peterson 1978). Large waterholes are a feature of several rivers in the Channel Country, such as Cooper Creek, the Diamantina and the Georgina, where they occur even along straight stretches (Mabbutt 1971).

Mound springs; *systems fed by carbonated water under hydrostatic pressure*

Water, taken in near the Great Dividing Range in Queensland, passes underground and rises under hydrostatic pressure through cracks in the overlying rock near the south-western edge of the Great Artesian Basin. These waters are high in calcium and bicarbonate and, as they reach the surface, half-bound carbon dioxide is lost, and calcium carbonate in the form of tufa or travertine is deposited (Bayly & Williams 1973). Over a long period, these deposits form substantial mounds around the springs.

The mound springs in north-eastern South Australia were semi-permanent oases in the desert and there is abundant archaeological evidence that they were of great importance to Aboriginal people (Boyd 1990). Only one of eight mound springs examined north of William Creek failed to provide evidence of large Aboriginal camp sites, and at Dalhousie Springs archaeological remains associated with one camp site extend for almost three kilometres. The Dalhousie Springs were an important water resource for the Lower Southern Arrernte people and the Wangkangurru people of the Simpson Desert (Potezny 1989).

Tree trunk hollows; *water accumulated in pockets of decay in trees above ground level.*

Lindsay (1893, p129) and Helms (1896), apparently in reference to the same incident observed during the Elder Scientific Exploring Expedition, described how an Aboriginal woman located and extracted water from a tree hollow. First she noticed a line of ants going up and down a tree, entering and emerging from a small knot-hole about shoulder-height from the ground. She then made a tube by removing the bark from a straight twig, using her teeth. Three or four of these tubes were then joined end to end and the long composite pipe was pushed through the hole in the knot and used as a drinking-straw to suck up the water trapped in the tree hollow. Where the opening to the water chamber was somewhat larger, an alternative procedure, described by Cairns (1859) and Smyth (1878, v2, p253), could be used; the Aborigine tied a bunch of grass to the end of a spear and dipped this into the water before pulling it out and squeezing the water out of the grass into a coolamon.

Magarey (1899) noted that the tree species most exploited by Aborigines for tree-hollow water was the desert oak (*Allocasuarina decaisneana*) and that such trees were as well known to the Aborigines of a region as were rock-holes (gnammas) and native soakage-wells. Bloodwood (*Eucalyptus terminalis*) may also have reservoirs in its trunk (Tietkens 1891). Kavanagh (1984, p6-5) found that the Ngatatjara [Ngaatjatjarra] People in the Warburton Ranges, used water stored in the trunks of old specimens of the cork tree (*Hakea macrocarpa*).

Tree roots; *water that flows from cut tree roots after excavation*

Magarey (1899) related the story of the noted explorer Tietkens expressing astonishment to an Aborigine that one of his kin could be generating a column of smoke away in the distance, in country that Tietkens had repeatedly visited and knew (or thought he knew!) to be absolutely waterless. The Aborigine at Tietkens's side responded, "He is all right. He got tree-water."

One of the earliest descriptions of Aborigines securing water from the roots of trees was that of Eyre (1845, v1, p350) who observed the procedure during his epic trek across the Great Australian Bight. Cairns (1859) provided a similar account of water recovery from the roots of mallee eucalypts in north-western Victoria. In brief, mallee roots when excavated, broken off and held vertically, dripped a clear, watery and highly potable fluid. In the desert regions of central Australia, the red mallee, *Eucalyptus socialis*, was the favoured species. However, either side of the Nullarbor Plain it was a different red mallee, *Eucalyptus oleosa*, that was exploited by natives for water (Cleland 1957).

Magarey (1899) pointed out that Europeans "have laid down under a 'water-tree' and died of thirst, whilst the water they so terribly needed lay only two or three inches under the scorching sand, and beneath their outstretched finger-tips. The aboriginal knows better." However, the apparently simple Aboriginal technique was not as easily imitable by Europeans as Magarey seemed to suppose. Helms (1896) noted that his own attempts to imitate the technique were often unsuccessful and Giles (1889, v1, p45) expressed similar reservations as follows:

> "A white man would die of thirst while digging and fooling around trying to get the water he might know was preserved by the tree, but not for him; while an aboriginal, upon the other hand, coming to a mallee-tree, after perhaps travelling miles through them without noticing [selecting] one, will suddenly make an exclamation, look at a tree, go perhaps ten or twelve feet away, and begin to dig. ....A very long root such as I have mentioned might give nearly a bucketful of water; but woe to the white man who fancies he can get water out of mallee."

The roots of water-mallees run out from the trunks for 10-20 metres and lie only 5-25 centimetres beneath ground level. An Aborigine would try the ground at about 2-3 metres from the trunks, or near a bulge or crack in the earth, and excavate the root with a wood shovel or spear-point. The root would be pulled up and broken off near the trunk, then pulled up towards its extremity, and broken into lengths of 50-100 cm. These lengths were then stood on end against the trunk to drain into a coolamon or marsupial-skin bag. If an Aborigine were very thirsty he or she would suck immediately on the cleaned end of a vertical root-stick. Roots about as thick as a person's wrist were said to be best. One water-mallee usually has from four to eight side roots running close to the surface, and one mallee root of average length would provide enough water for the immediate needs of two or three thirsty natives (Magarey 1899).

The desert kurrajong (*Brachychiton gregorii*) is another especially good water-tree, its roots being very porous and yielding water very freely. Needle-bush (*Hakea leucoptera*) and the desert oak (*Allocasuarina decaisneana*) were further useful providers (Magarey 1899). To these should be added water bush, *Grevillea nematophylla* (Kavanagh 1984).

Dew; *water collected from vegetation in the form of dew droplets*

Magarey (1899) described how Aborigines would go out before sunrise and collect dew-drops with a sweep of the arm or movement of a stick. A more efficient method was to form a ball of grass and use this as a sponge to gather the dew lying on grass. The water would then be squeezed out of the ball into a coolamon or pitchi (Tindale & Lindsay 1963, p64). Another method was to hold a water container under the dew-drenched twigs of a shrub or tree which was tapped or shaken. The leaves of the sandalwood tree (*Santalum spicatum*) were said to be particularly useful for gathering early morning dew. Aborigines in central Australia collected dew from the desert heath myrtle, *Thryptomene maisonneuvii*, to make a sweet drink.

Frogs; *water contained within the body of frogs*

Carnegie (1898, p.17) recorded the following yarn told to him by a friend at a bush camp:

> "He [Carnegie's friend] was perishing from thirst, and, at the last gasp, he came to a clay-pan which, to his despair, was quite dry and baked hard by the sun. He gave up all hope; not so his black-boy, who, after examining the surface of the hard clay, started to dig vigorously, shouting, 'No more tumble down, plenty water here!' Struggling to the side of his boy, he found that he had unearthed a large frog blown out with water, with which they relieved their thirst. Subsequent digging disclosed more frogs, from all of which so great a supply of water was squeezed that not only he and his boy, but the horses also were saved from a terrible death!"

Although laughed off at the time by most of Carnegie's companions, the essentials of the story were, as Carnegie himself realized, factually based.

Spencer & Gillen (1912, v1, pp58-62) provided a good account of the behaviour and ecology of the water-holding frog (*Cyclorana platycephala*), which has the ability to take up a large amount of water (stored in the bladder) before burrowing beneath the surface of a claypan where they may aestivate for more than a year. They described how their native guide had the uncanny ability to appreciate the significance of some indistinct marks on the surface and how they cut into the rock-hard clay with a hatchet to recover one of these frogs at a depth of about 30 centimetres. It was a common practice for Aborigines to squeeze the body water out of this frog and drink it. In the words of Waite (1929), "water may be obtained by squeezing the body of the frog, and the Australian native will win through where unattended white men would perish of thirst". A graphic account was given by Basedow (1935, pp86-7) as follows:

> "My amazement reached a climax when he [an Aboriginal escort] seized the frog, placed the head-end in his mouth and squeezed its body. And while he squeezed he drank! It was not a mere sip, either; I should say the fluid he swallowed would have been sufficient to fill a teacup. As he drank, the old fellow looked at me out of the sides of his eyes in a very quizzical way; and when he had drained this most remarkable goblet to its last drop he smacked his lips afresh and exclaimed 'Bullya Marra' ['Good! Good!']."

The yield of fluid claimed in this quotation (*ca* 200 ml?) is probably exaggerated, since Tyler (1982) quoted a volume of only 10-25 ml. However, Kavanagh (1984) pointed out that the water-holding capacity constantly changes and that volumes range from one teaspoon to half a teacup [say 5-100 ml]. A yield of 100 ml is beyond the capacity of *C. platycephala* and may refer to *C. australis*. Not only was the body water drunk but the remainder of the frog was then eaten!

Apart from the observation of marks on the surface of a claypan, Aborigines could also detect the hidden chambers of aestivating *Cyclorana platycephala* by tapping on the hard surface with the butt of a spear (Basedow 1935; Goodhart 1939; Charnley 1954). A further method, useful after a long period of drought, was to stamp on the ground and listen for the faint croaking of the frogs (Tindale & Lindsay 1963; Cleland 1966).

Discussion

The first six of the above listed specific sources of water (gnammas, soaks, impoundments, claypans, riverine waterholes, mound springs) may all be grouped as surface water resources. The longevity of these range from the highly ephemeral small claypans (Gilgai) and larger claypans, through to the more reliable and often quasi-permanent soakage-wells. It was these mainly small-scale surface waters on which desert Aborigines principally relied. Other conceivable water sources, such as lakes, rivers and creeks, have been deliberately omitted from this review on the grounds that they were rarely significant in the context of Australian deserts. Although maps of these regions show them dotted with lakes and playas, and crossed by rivers, most of these are either dry or saline most of the time. With respect to survival waters in Australian deserts the general rule is that big is not beautiful! Water resources other than surface water, such as those from tree trunks and roots, dew and frogs, were very important to certain tribes such as the Ngalea (Tindale 1974, p215) and to people in transit (Cleland 1966).

Gould (1991) discussed two alternative means whereby Ngatatjara [Ngaatjatjarra] Aborigines in the Western Desert survived when stressed by drought. The first strategy, "drought escape", was adopted in response to long periods of absolute drought, and involved the abandonment of home areas and migration over long distances to join relatives already living in areas with an adequate water supply. Although Gould did not directly observe this pattern of behaviour during his 5-year study, he gathered indirect evidence from the Warburton Ranges Mission and various groups of Ngatatjara people that earlier severe droughts had resulted in the temporary evacuation of drought-stricken regions. The second strategy, "drought evasion", involved the continuous occupancy of the home area and reliance on the more reliable water supplies such as soakage-wells. Use of this strategy by the Ngatatjara was widely observed by Gould (1991) during 1969 and 1970. In regions with reliable water supplies, Aborigines may have relied exclusively on drought evasion. This is thought to have been the case for those living in or near the Everard Ranges (Tindale 1974; Gould 1991).

Despite their extraordinary water-locating skills, desert Aborigines had no absolute guarantee of survival. Cane (1990) noted, with respect to the Western Desert, that, "Almost every Aboriginal person I have spoken to can recall times when they were close to death - or members of their immediate family had died in attempts to find water during the critical phase of a prolonged dry season". In the late 1940's a group of Aborigines were trapped at a disappearing waterhole west of Lake Mackay. These people knew of two waterholes that may still have had water; one was to the north, the other to the south. Accordingly the party split into two; those going north survived, but the southern group found their waterhole dry and perished (Cane 1990). A further example was provided by Gould (1969) who described a region between the Warburton Ranges and the South Australian border with few reliable water sources and in which Aboriginal deaths occurred during seasons of marginal rainfall.

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Reproductive ecology of the black-headed goanna *Varanus tristis* (Squamata: Varanidae)

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Abstract

The black-headed goanna, *Varanus tristis,* oviposits in October and November in the western Great Victoria Desert; the eggs are layed in a hole that the female digs in the ground. Neonates hatch toward the end of summer. Body colour and pattern of neonate *V. tristis* differ appreciably in the western Great Victoria Desert from adults, and changes to the adult pattern after a couple of months. Clutch size for *V. tristis* is best predicted from body mass, although there is also a significant relationship between clutch size and snout-to-vent length. An inter-specific regression equation for the *Odatria* subgenus is a much more accurate predictor of clutch size for *V. tristis* than a regression equation that includes data for goannas of other subgenera. Fat bodies of males decrease in size during December and January then increase during February and March; they are largest during September and October. Combined testis length decrease from appropriately 11% of snout-to-vent length (SVL) during the breeding season in early summer to 5% of SVL in February.

Introduction

Relatively little is known about the breeding biology of the black-headed goanna *Varanus tristis* (Pianka 1971, 1986, 1994; Christian 1981; Broer & Horn 1985; Eidenmüller 1989). The breeding season is from September to October (Pianka 1971), and mean clutch size is approximately ten (James *et al.* 1992; Pianka 1994) but nothing has been reported on oviposition sites. There are two reports of *V. tristis* being bred in captivity (Broer & Horn 1985; Eidenmüller 1989).

This paper reports on the breeding behaviour of *V. tristis* in the western Great Victoria Desert, an oviposition site, variation in neonate body colour and pattern, the effect of SVL and body mass on clutch size, and seasonal cycles in testis and fat body size.

Methods

Observations on breeding behaviour were made during a larger study of activity areas and daily movement patterns for *V. tristis tristis* during the breeding season in the western Great Victoria Desert (Red Sands, 28° 12' S, 123° 35' E). The site is a complex mosaic of sandridges and interdunal flats with a vegetation of spinifex (*Triodia basedowii*), marble gum trees (*Eucalyptus gongylocarpa*), mallee trees (*Eucalyptus concinna*), acacia (*Acacia aneura* and others) and other small bushes and grasses. Location and daily movements of twelve *V. tristis* were monitored between 11 September and 8 November, 1995, in the western Great Victoria Desert using miniature radio-transmitters attached to the side of the base of the monitor lizard's tail or surgically inserted into their abdominal cavity. One female *V. tristis* became gravid and layed eggs during this period.

Notes were maintained of evidence of courtship and breeding behaviour, *e.g.* males following scent trails, pairs together and hole digging activity. Spoor were also used to determine movement patterns. We also dug up one nest and removed eggs to hatch in an incubator. The incubator was maintained at about 29 °C and the eggs were placed in a mixture of vermiculite and water at the ratio 1:1 based on mass. This enabled us to measure neonate size and estimate incubation time.

Clutch size, maternal body mass and SVL of gravid females were recorded from an examination of 24 *V. tristis* captured opportunistically since 1967 in the arid interior of the Great Victoria Desert. Lengths of fat bodies were recorded for 63 males and 37 females captured since 1967 in the same general area. The combined length of testes is reported for 62 males.

Results

A male and a female *V. tristis* were found one behind the other in a hollow log on 15 November 1978. This male's testes measured 13 mm and 14 mm and the female contained 8 shelled eggs in the oviducts. On 30 October 1990, a mating pair was found together in a marble gum tree, the female had sperm exuding from her cloaca. A male *V. tristis* was seen lying on a female *V. tristis* under a spinifex bush on 1 October 1995 and both lizards were found in a hole in the ground on 2 October 1995. There was no evidence to indicate this hole had been dug by these *V. tristis* (*i.e.* no fresh scratchings). Other female *V. tristis* were seen in holes, or were seen digging holes on 13, 14, 24 and 26 October 1995. All females captured with a male had a white powder stain on the dorsal surface of

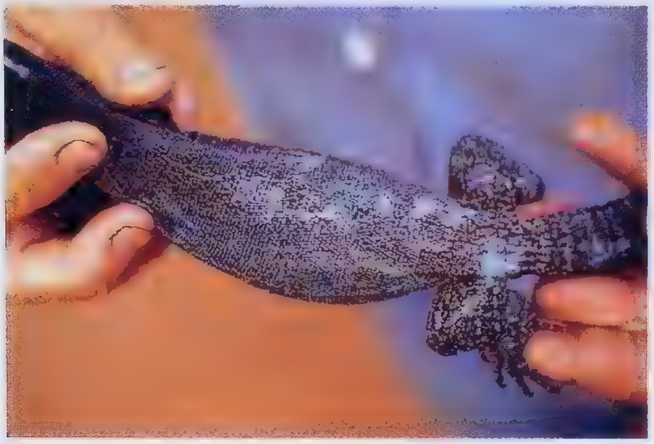

Figure 1. White powder stains on the dorsal surface of a female *V. tristis* during the breeding season and dorsal colour pattern.

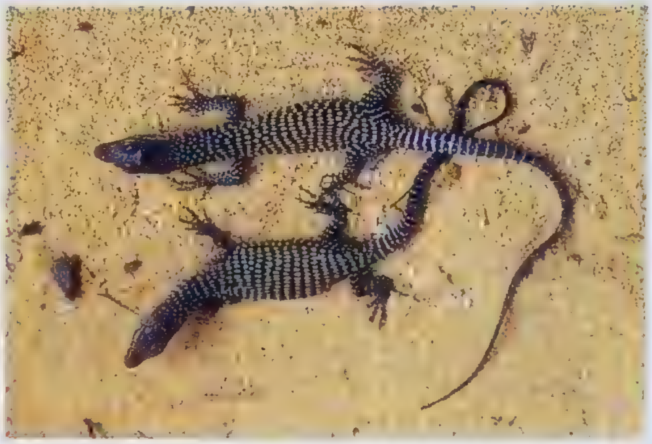

Figure 2. Body pattern of neonate *V. tristis* from the western Great Victoria Desert.

their pelvic area, generally between their hind legs and mid-way up their backs (Fig 1).

One female *V. tristis* (mass 210 g, SVL 235 mm) was seen digging a hole in the base of the stump of a dead (burnt to ground level) marble gum tree on 17 and 18 October 1995. This *V. tristis* was again seen at the hole on 21 and 22 October 1995 when it back-filled the hole suggesting that it oviposited about 21 October 1995. Eggs were located in the burrow about 20 cm below ground surface. The female had burrowed down inside the hollow trunk and then dug through an underground hole in the dead tree trunk that would have been just large enough to get its body through. Eggs were deposited in a junction between a dead root and the basal bole of the dead gum tree. An initial attempt was made to excavate the nest chamber on 7 November 1995 but the eggs could not be found. Disturbance to the soil near the eggs may have damaged two eggs, described below to have hatched prematurely. Ten eggs were excavated from the nest on 21 January 1996; one of the eggs was desiccated and failed to develop. The other eggs were returned to the laboratory and incubated at about 29 °C. Two eggs hatched on 3 and 5 February; they appeared to be premature, as the hatchlings were small [3.2 g, SVL 67 and 68 mm, total length (TL) 163 mm]. These two neonates died within 24 hours of hatching. The remaining seven eggs hatched between 12 and 15 February, an incubation period of 114 - 117 days; these hatchlings were 4.3 g (± SD 0.31) and had a SVL of 72.7 mm (± SD 5.12), and a TL of 181.7 (± SD 11.54)] and grew rapidly. SVL increased by 40% in the first 17 weeks of captive life, compared with 30% for *V. eremius* and 18% for *V. brevicauda* during a similar period in captivity (Thompson, *unpublished observations*).

As occurs in many species of *Varanus*, neonate *V. tristis* have a markedly different colour and pattern from adults (Bennett 1993, 1996). Adults in the western Great Victoria Desert have a dark grey-to-black head, neck, forelegs and most of the tail. The back has a fine reticulum of elongated black-centred red-brown circles (Fig 1). The proximal end of the tail is ringed with greyish-white flecks that fade in larger individuals. In contrast, neonate *V. tristis* from this site have a dark grey head with a broad black stripe through the eye. From the neck to about half way down the tail, the body is encircled by rings of closely spaced, small, white-to-yellow dots (Fig 2). Fore- and hind-limbs have rings of less closely spaced, small, white dots. This colour pattern changes to that of the adult form during the first two months of life.

We examined 24 *V. tristis* with either enlarged yolked ovarian eggs or shelled eggs in their oviducts. Mean clutch size was 9.8 (± se 0.57), mean SVL of gravid females was 246.6 mm (± se 4.13) with a minimum SVL of 199 mm. Mean body mass of gravid females was 203.9 g (± se 10.9) with minimum mass being 86 g. Combined (left and right) testes length and combined fat body length as a proportion of SVL for 63 males and combined fat body length for 37 female *V. tristis* are shown in Figure 3. There is a significant difference in combined testis length as a proportion of SVL (ANOVA, $F_{7,55} = 9.86$, $P < 0.05$), and combined fat bodies length as a proportion of SVL (ANOVA, $F_{7,55} = 4.71$, $P < 0.05$) for males among months (August to March). Data for months other than October and November are insufficient for a similar analysis for females. The size of male testes is comparatively larger during August (from 22nd) to November (combined testes length / SVL = 0.105, ± 0.0023) and declines from December to March (0.075, ± 0.0032). Combined fat body length as a ratio of SVL declines from 0.43 (± se 0.019) for male *V. tristis* in August and September to 0.32 (± 0.023) in October, 0.31 (± 0.034) in November to 0.16 (± 0.011) in December. It then increases from January (0.28, ± 0.047) through to February and March (0.34, ± 0.034). The size of fat bodies in August and September suggests that male *V. tristis* are foraging during autumn and possibly winter. In females, fat bodies during late summer seem to be a similar size to those prior to the breeding season, although late summer data are limited (Fig 3).

The intra-specific allometric relationship between clutch size and body mass and SVL is represented by the following two equations:

$$\text{Clutch size} = 2.6\ (\pm 1.73) + 0.035\ (\pm 0.0082)\ \text{mass (g)}$$

$$(r^2 = 0.43,\ F_{1,21} = 18.33,\ P < 0.05), \text{ and}$$

$$\text{Clutch size} = -9.0\ (\pm 6.03) + 0.076\ (\pm 0.0244)\ \text{SVL (mm)}$$

$$(r^2 = 0.28,\ F_{1,21} = 9.76,\ P < 0.05).$$

The relationship between SVL and clutch size for ovarian and oviductal eggs is shown in Fig 4.

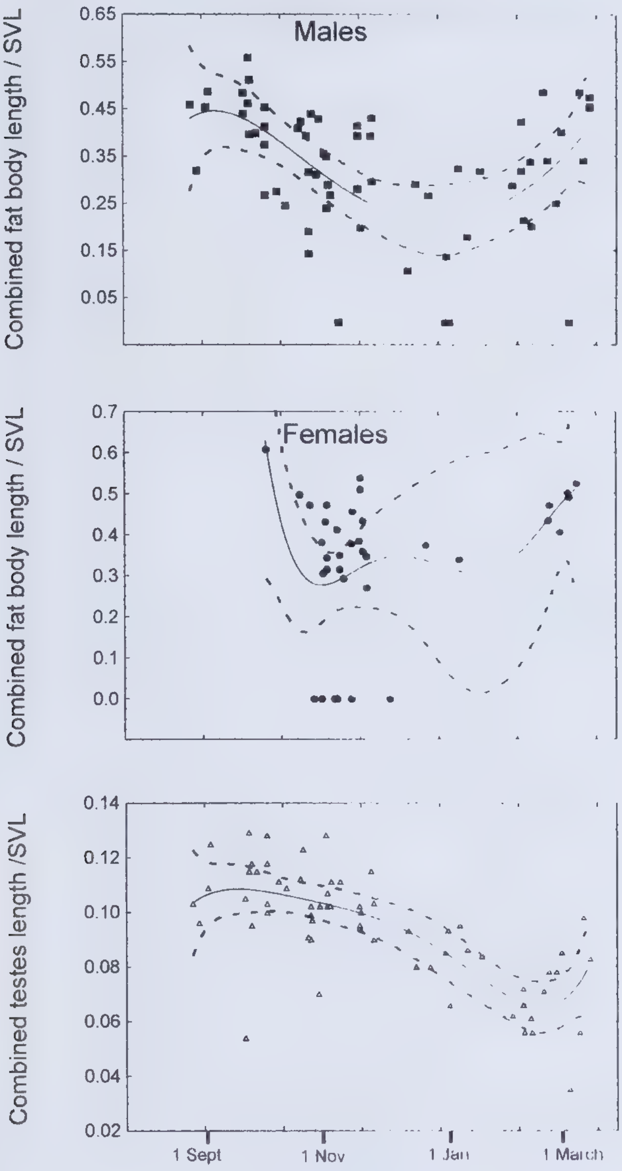

Figure 3. Changes in the size of fat bodies and testes for *V. tristis* over the year. Values are the ratio of combined fat body length/SVL, or combined testes length/SVL. Solid curved lines represent the best-fit polynomial equations; the dotted lines indicate the 95% confidence limits.

Discussion

Movements and locations of male *V. tristis* were dominated by their proximity to females during the breeding season. During the mating season, males spent most time in a tree hollow directly behind a female or moving between a couple of females within their activity area (Thompson *et al.* in press). Male *V. tristis* that had located a female positioned themselves behind the female in a tree hollow, perhaps to block her exit. This is possibly a strategy to stop the female moving to another site and perhaps mating with another male, or alternatively to limit access of other males to the female while she is in the tree. *Varanus tristis* appears to be polygamous, since most males visited at least two females in their activity area (Thompson *et al.* in press). Tracks indicated that males moved in a direct line between females rather than returning to a female's last known location. Spoor, presumably of a male, was observed to change direction abruptly to follow the spoor of another *V. tristis* (presumably a female; see Tsellarius and Men'shikov 1994) on numerous occasions. *Varanus tristis* spoor often indicated that one *V. tristis* had followed another for distances up to 100 m. Tracks of the second *V. tristis* were always almost directly on top of the first. One male *V. tristis* was observed to travel 723 m in an almost direct line in one day, into the wind, and was found the next day in a dead upright tree with a female (Thompson *et al.* in press). Male *V. tristis* probably follow scent trails carried by the wind to find females.

Our observations on digging and egg laying activity suggest that females oviposited from mid to late October. This is earlier than reported by Pianka (1982) for 11 other *V. tristis* captured during 1978 and 1989 at the same and another site approximately 130 km west (Pianka's L area 28° 31′ S, 122° 46′ E). Different environmental conditions in 1995 may have advanced the breeding season, or alternatively other unmonitored *V. tristis* may have oviposited later in 1995. To find a possible climatic variable that may have advanced the breeding season for *V. tristis* in 1995, a comparison of minimum and maximum daily temperatures, and total rainfall for the three months preceding oviposition (July, August and September) at Yamarna (8 km west of the study site) indicates a significantly higher maximum daily temperature for both July and August in 1995 compared with 1978 and 1989 (Table 1). These higher maximal temperatures may have resulted in an early emergence of *V. tristis* from their winter inactive retreats and thus brought forward the breeding season.

There are no reports of *V. tristis* normally frequenting or digging holes in the ground, although they have been reported to hide under concrete slabs and water tanks (Christian 1981; Brunn 1982). Similarly, no data have ever previously been reported on nesting sites for this species of goanna. Pit-trapping in the area by Pianka (1994) during late February and early March in 1991 resulted in the capture of only one neonate (72 mm SVL) on 3 March 1991. The early-to-mid February hatching of *V. tristis* eggs laid in mid October is comparable to the

Table 1

Minimum, maximum temperatures and rainfall for Yamarna in July, August and September, 1978, 1989 and 1995.

Variables	1978	1989	1995	P value
July				
Minimum (mean °C)	6.6	2.9	4.2	< 0.05
Maximum (mean °C)	16.9	16.9	19.2	< 0.05
Rain (total mm)	16.0	8.6	20.1	0.56
August				
Minimum (mean °C)	7.6	4.7	5.3	< 0.05
Maximum (mean °C)	19.4	20.1	23.5	< 0.05
Rain (total mm)	46.4	0.0	0.0	< 0.05
September				
Minimum (mean °C)	8.0	9.0	8.9	0.44
Maximum (mean °C)	21.9	26.0	26.5	< 0.05
Rain (total mm)	13.4	0.0	5.0	0.16

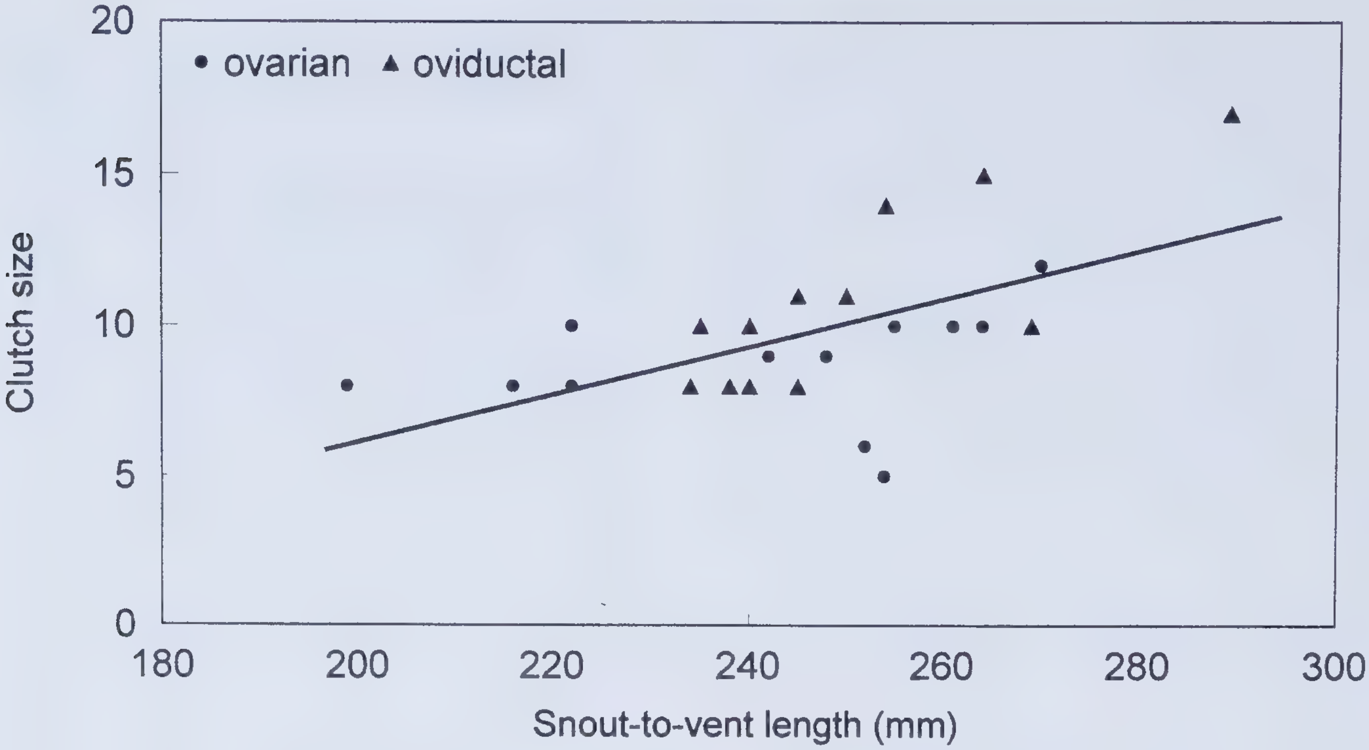

Figure 4. Relationship between the number of ovarian and oviductal eggs and SVL for *V. tristis*. The line is for all points; the equation is CS = 8.98 + 0.76 SVL (mm).

incubation time for other similar-sized monitor lizards (Horn & Visser 1989, 1997). Eidenmüller (1989) reports the incubation time for *V. tristis orientalis* eggs to be between 116 - 136 days at a temperature of 27.5 °C (± 0.5 °C). Therefore eggs laid in November (Pianka 1982, 1994) would probably hatch in March. Adult *V. tristis* are very seasonal in their movement with the majority being seen and tracked in October and November (Pianka 1994). Movement drops off abruptly in December and January, as judged by the presence or absence of tracks. Whether hatchlings remain active during their first winter, or whether they gather sufficient resources during later months of summer to sustain them over a cold winter period of inactivity is unknown. However, a 9 g juvenile was captured in the Perth area foraging in July and captive neonates hatched from eggs taken from this study site were active on warm winter days in an outdoor cage. Three arboreal odatrian goannas from central Western Australia, *V. caudolineatus*, *V. gilleni* and *V. tristis*, all oviposit in Spring (*V. gilleni* 28 October and 1 November - Thompson, *unpublished observations*, and James *et al.* 1992; *V. caudolineatus* 22 September and 12 October - Thompson, *unpublished observations*; *V. tristis* 21 October - this study, late November - Pianka 1982). Based on the summary of Horn and Visser (1989, 1997), all three species would hatch towards the end of summer.

The greater length of fat bodies in *V. tristis* in spring compared with late summer suggest that they forage and deposit fat during autumn and winter. The relatively shorter length of fat bodies of females during October to December probably reflects their energy contribution to the production of eggs. Thus, females appear to rely on fat reserves accumulated during the previous summer and autumn as the principle energy source for their clutch. The decline in the male's fat body size during the breeding season is probably due to their preoccupation with mating rather than feeding. During the breeding season (August - November), testes are comparatively larger. Testes decrease in size from December to a low in March (Fig 3). We have no data on when testes size begins to increase.

Clutch size for *V. tristis* can best be predicted from body mass [CS = 2.6 + 0.035 mass (g)]. Comparable intra-specific regression equation data to predict clutch mass from SVL or body mass for other varanids are not available. The clutch size of 10 for the female that we monitored laying eggs agrees with the predicted clutch size based on body mass (210 g) but is greater, by one, than the that predicted from SVL (235 mm). Figure 4 shows the variation in clutch size at any particular SVL.

Based on the inter-specific regression equation of James *et al.* (1992) for Australian *Varanus* spp, clutch size = 0.03 $\mathrm{SVL}^{1.01}$ (without *V. semiremex*, *V. giganteus*, *V. varius*) an average female *V. tristis* with a 235 mm SVL would be expected to have a mean clutch size of about 7.4 eggs. This is appreciably below the mean for this species of 9.8; only two of the 24 gravid female *V. tristis* examined had a clutch of 7 or less eggs. However, if only the Odatrian data from James *et al.* (1992) are included in the regression equation, clutch size = 0.004 $\mathrm{SVL}^{1.44}$ (r^2 = 0.9; Fig 5) and the predicted clutch size for *V. tristis* is 10.4, closer to the actual species mean. Thus, the relationship between body length and clutch size could differ between the two subgenera (*Odatria* and *Varanus*).

The significance of the white powder stain on the dorsal surface of the lower back and pelvic area of females (Fig 1) is unknown and merits further investigation. One likely explanation is that it is uric acid rubbed on the female by the male prior to mating.

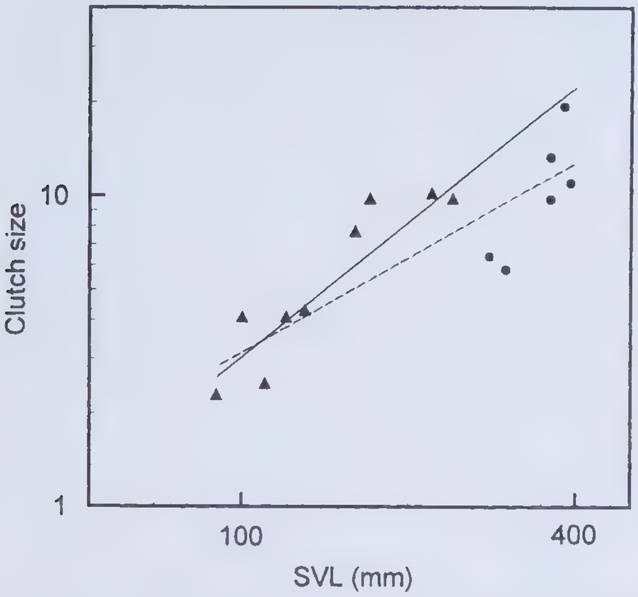

Figure 5. Relationship between snout-to-vent length and clutch size for varanids (from James *et al.* 1992), with regression lines for all species (dotted, James *et al.* 1992) compared with the regression line for odatrian (solid line; triangles) goannas.

The body surface colour and pattern of neonate *V. t. tristis* in the western Great Victoria Desert differs from that of *V. t. orientalis,* which have a pattern very similar to adults. Neonate varanids often are more colourful than adults (King and Green 1993). Why the pattern only persists for a couple of months is unknown.

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Bornhardt inselbergs in the Salt River Valley, south of Kellerberrin, Western Australia (with notes on a tesselated pavement in granite and pinnacles in laterite)

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Abstract

Several prominent bornhardts, or dome-shaped granitic hills, occur in or near the valley of the Salt River, south of Kellerberrin, Western Australia. They originated as subsurface bedrock rises projecting into the base of a regolith produced by fracture-controlled weathering beneath a lateritised land surface in Cretaceous and earlier Mesozoic times. They were exposed during the Early Cainozoic by the stripping of the regolith by a rejuvenated Salt River and its tributaries. By the Miocene, the river had cut a bedrock gorge below the present valley, but this has since been infilled and buried. Some effects of weathering by and in the lateritic carapace are noted.

Introduction

The Salt River is part of a complex system of palaeochannels known as the Yilgarn River catchment (Salama 1997), which drains to the Indian Ocean via the Swan River and which occupies an area of about 130000 km^2 in the south-western part of the Archaean Yilgarn Craton of Western Australia. Although it usually comprises a few narrow channels and with every appearance of being sluggish, in flood the river occupies a wide channel. The present broad flood plain, with several narrow individual channels could be the trace of an old meander belt, but if the channel indicates the former extent of the river then its geometry suggests a high (flood?) discharge, possibly related to a Miocene or Pliocene period of higher rainfall (*e.g.* Kemp 1978; see also Salama 1997). South of Kellerberrin the river flows from east to west, and its valley is incised some 100 to 120 m below the level of the high plain surface of the interfluves to the north and south.

Several prominent granite hills occur in and adjacent to the Salt River Valley. With two exceptions, they are basically domical in form, although the geometry of the domes varies from elongate, as with Mt Stirling, Tutakin and Gundaring hills, to dome-on-dome (or "cottage loaf") at Kokerbin Hill, to a simple hemisphere at Middle Dome, between Mt Stirling and Gundaring. Known in different parts of the world as demi-oranges, meias laranjas, dwalas, morros, matopos, and ruwares, they are here referred to as bornhardts, after the German scientific explorer of that name (Bornhardt 1900; see also Willis 1934; Twidale 1982a; Campbell 1997). The exceptions are Nangeen Hill, which is a block- and boulder-strewn nubbin or knoll, and a small residual between Mt Stirling and Tutakin Hill which similarly consists of a scatter of blocks and boulders, on a low rise. Whatever their morphology, they stand in isolation, so that all these residuals are also inselbergs or "island mountains".

A block is an angular rock mass, usually cubic, quadrangular or rhomboidal, but a boulder is more-or-less rounded and at least 25 cm diameter. Boulders differ from what have informally been called haystacks or pillars (*e.g.* Twidale & Campbell 1984) in that the latter remain in physical continuity with the underlying rock mass, whereas boulders are detached. In the Salt River Valley the major divides are broad and rolling. Large areas are covered by what appears to be a thin regolith separating extensive rock platforms or low large-radius domes, many of them with a scatter of blocks and boulders. Such assemblages are natural. There is no suggestion that they were constructed or reorganised by humans for interment or, indeed, any other purpose. There is, therefore, no justification for calling them tumuli (Main 1997 p115), for a tumulus (or barrow) is a stone-lined burial chamber covered by debris and looking like a low, smooth, rounded, frequently elongate hill.

The term "tor" has been applied to both boulders and bornhardts (*e.g.* Williams 1936; Hills 1940 pp26-28; Cotton 1948 p30; Mabbutt 1952; Thomas 1965; Main 1997) but, increasingly, it is recognised that "tor" is a regional British term applied to steep-sided angular or castellated hills ("about the size of a house"; Linton 1952, p354). It is not apposite to any of the forms discussed in this paper, most of which are bornhardts; which are moreover the basic forms from which both nubbins and castle koppies evolve (Twidale 1981). The origin of such domical hills has long been the subject of vigorous debate (for reviews, see Twidale 1982a,b; Vidal Romani & Twidale 1998). The residuals discussed here take on a special significance because they occur in a setting that allows their evolution to be reconstructed and their age to be determined. This study is dedicated to an analysis of the origin of these forms, though the origin of several other features is also broached.

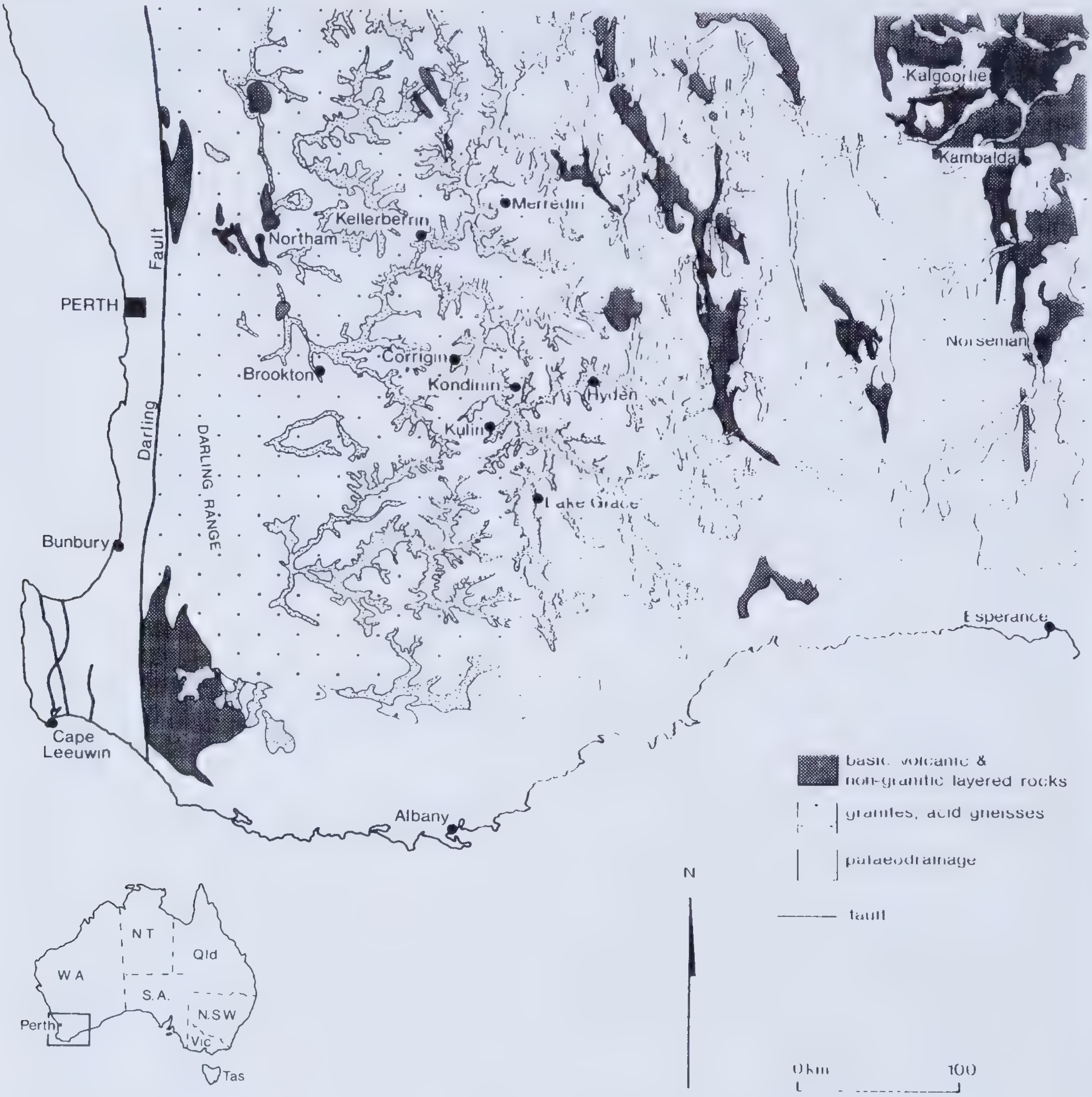


Figure 1. Geology and palaeodrainage in south-western Western Australia (modified from Anon 1975; Commander 1989).

Geological and Topographical Context

The Yilgarn Craton (Fig 1) is one of the Western Cratons of Australia (Palfreyman 1984). In the south, in the area known as the Wheatbelt, Archaean gneiss and granite dating from about 2.64 Ga (Myers 1993; Nemchin *et al.* 1994) are dominant, though there are minor but economically important NNW-SSE trending bands of "greenstone" which consist predominantly of metamorphosed basalt, dolerite and other basic rocks (Fig 1). The area is traversed by prominent NW-SE fracture zones (lineaments) of latest Archaean or earliest Proterozoic age, with ENE-WSW and latitudinal trends also well represented. All have influenced stream development and hence stream patterns (Fig 2). Both in Zimbabwe and in Western Australia, such granitic bodies are conventionally regarded as being diapirically emplaced into flat-lying greenstone sequences (MacGregor 1951; Anhaeusser 1984; Hickman 1984) but Myers & Watkins (1985) attribute the outcrop patterns of the Yilgarn to the simultaneous deformation of greenstone and granites in large-scale fold interference dome-and-basin structures.

The Salt River area is dominated by outcrops of a medium and coarse-grained, in places porphyritic, adamellite (Muhling & Thom 1979; Chin 1986). The high plains to either side of the Salt River Valley are underlain by laterite, the lower by alluvium, with granite exposed, typically in large radius bornhardts, on the slopes

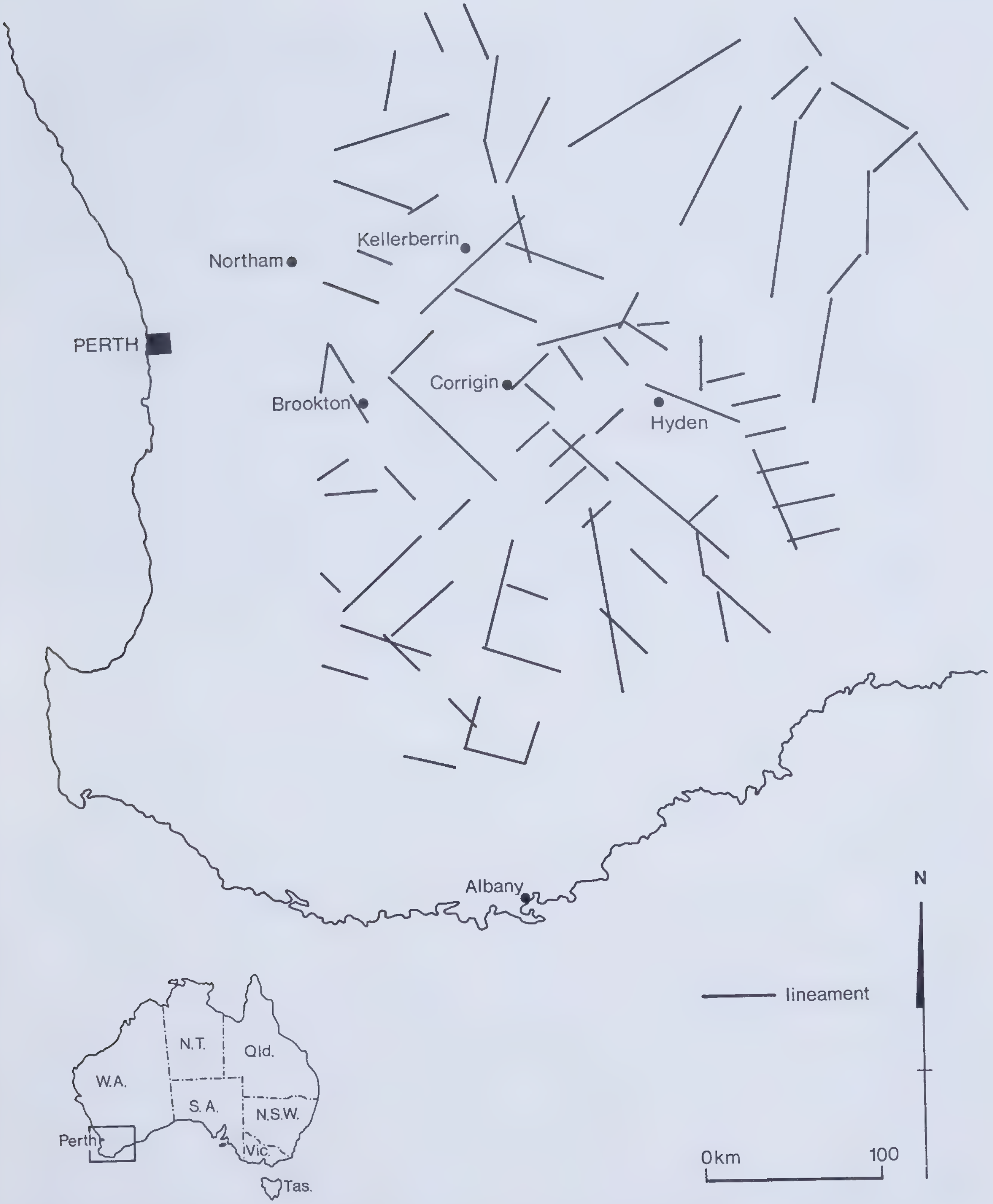


Figure 2. Inferred fractures (lineaments) in the southern Yilgarn Craton. Many are exploited by rivers (*cf* Fig 1).

between the two (Fig 3). Mt Stirling, Mt Caroline, Gundaring Hill, Tutakin Hill, Nangeen Hill and Kokerbin Hill are especially prominent domes exposed within or close to the channel of the Salt River.

The weathered mantle which underlies the high plains is well exposed at the low mesa informally referred to as Repeater Hill, where a thin (5 m) profile of primary laterite is exposed in a shallow quarry and in natural bluffs (Fig 4). It consists of a thin (up to 5 cm) sandy A-horizon overlying a pisolitic ferruginous zone about a metre thick, and underlain by about 4 m of kaolinised granite which grades down into weathered bedrock. The pisolitic zone is exposed in a bluff in which are scored cyclindrical tubes or pipes up to 15 cm diameter. That

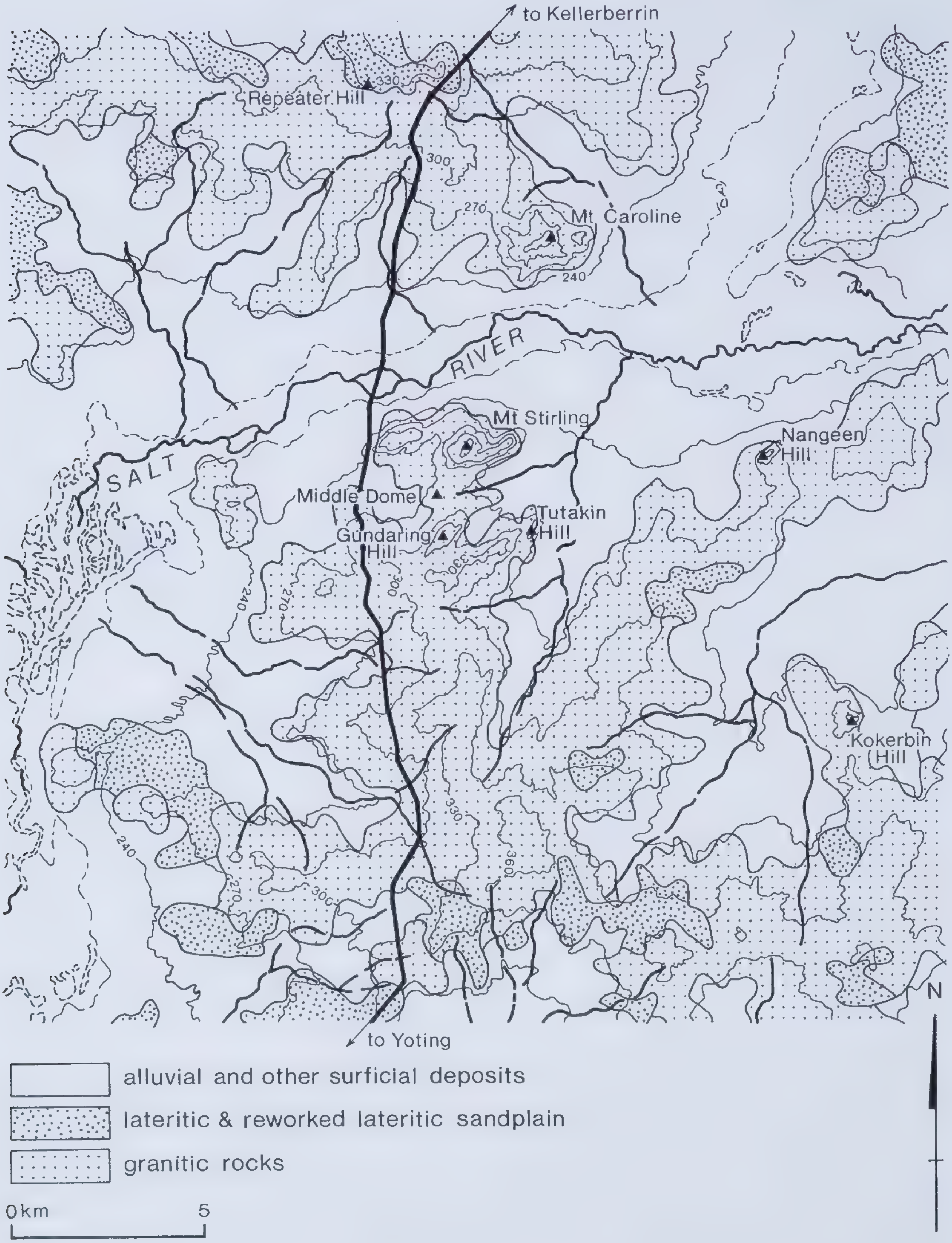


Figure 3. Major geological and topographical features of the Salt River Valley and environs (modified from Series R712 Sheet 2435-III *Pantapin*. Edition 1 - LSWA; Geological Series Sheet SH 50-15 *Kellerberrin*. Geological Survey of Western Australia).

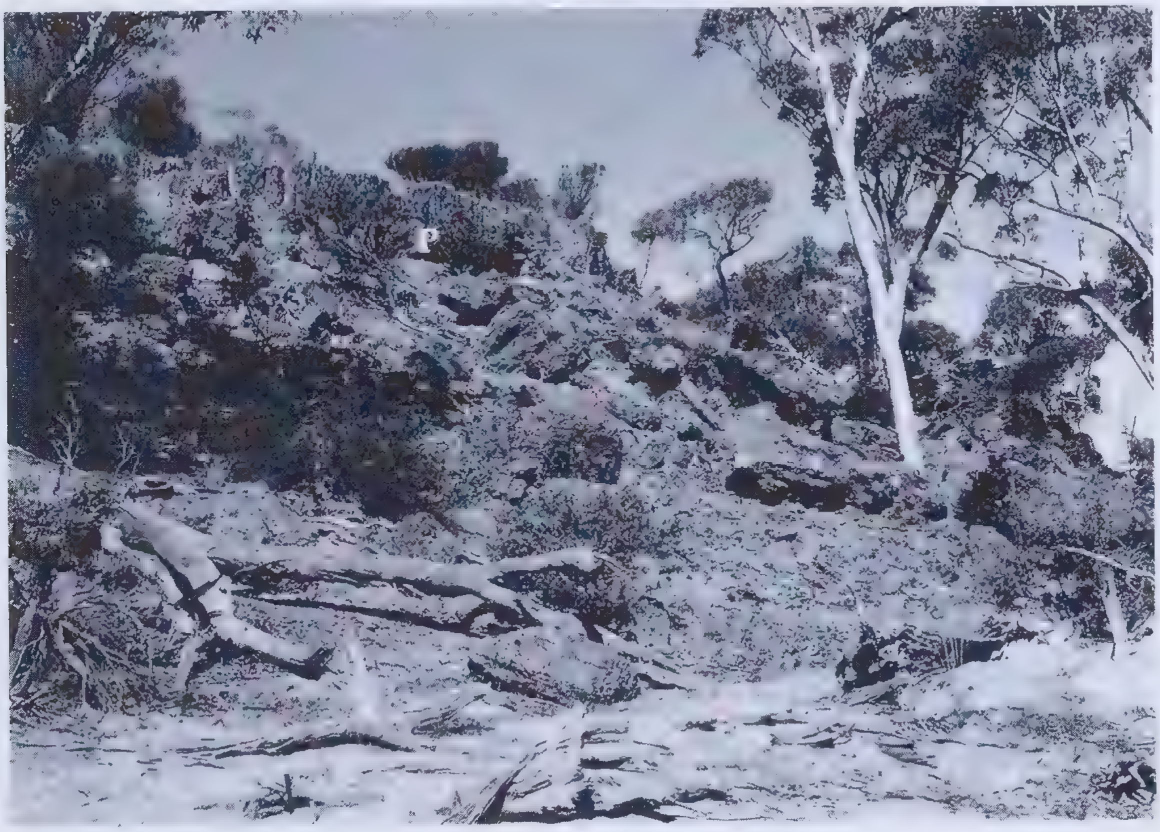


Figure 4. Laterite exposed at Repeater Hill. P: pisolitic zone, overlying kaolinised rock in scarp, and weathered granite at scarp foot.

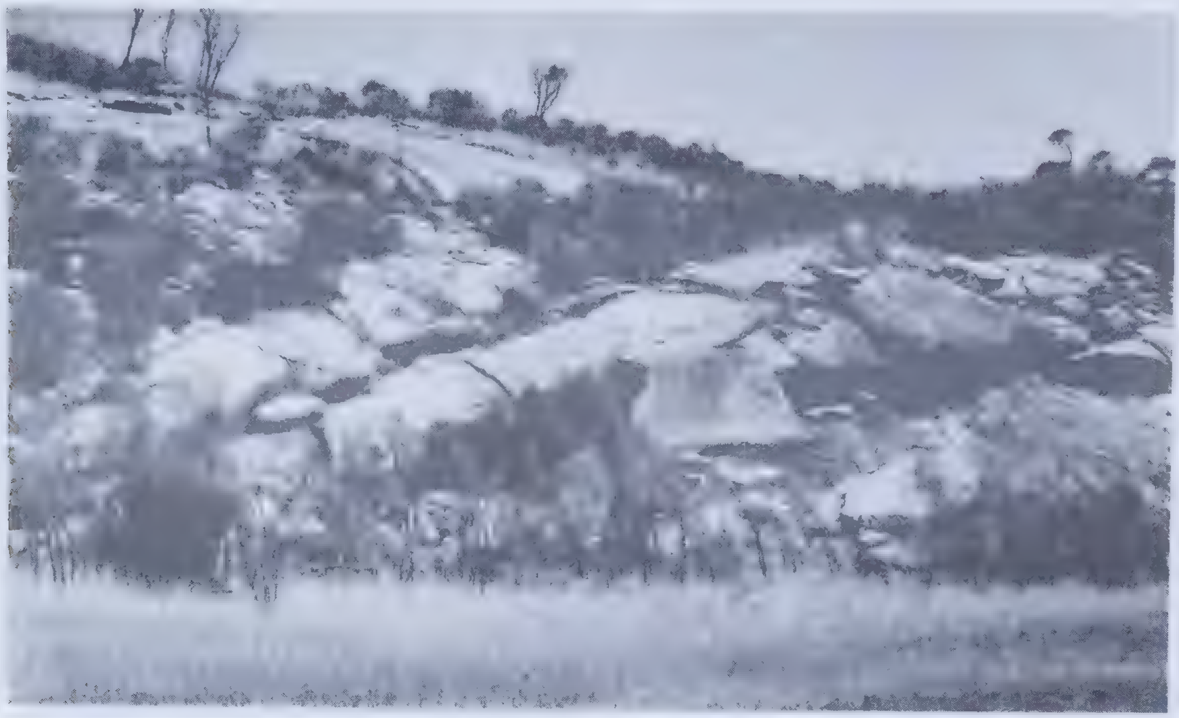
much of the ferruginous zone is penetrated by such pipes is suggested by the presence of hollows filled with sand and pisolitic detritus on the surface of the mesa.

Morphology of the Bornhardts

All of the Salt River Valley bornhardts display well-developed sheet structures, or thick slabs defined by parallel arcuate fractures. Many of them, as at Kokerbin Hill, and Gundaring-Tutakin, are so steeply dipping that there has been failure and slippage (Fig 5). Large residual blocks and boulders (some of them perched or balanced), rock basins and Rillen (gutters and flutings), fracture-controlled clefts (also known as Kluftkarren, and slots in the USA), largely enclosed hollows or tafoni developed on boulders and under sheets (some of the latter with collapsed roofs), cliff-foot caves, and flared slopes are also well and widely represented (Fig 6). A-tents, or pop-ups, (Fig 7A) and displaced slabs are also developed. Numerous minor fault displacements have been noted. Siliceous speleothems (Fig 7B) are abundantly developed at several sites (Vidal Romani *et al.* 1998).

- Mt Caroline is a bevelled bornhardt. The crest, averaging 310 m asl (above sea level), is boulder-strewn and at 340 m asl its blocky summit stands some 90-100 m higher than the adjacent plain. A minor boulder-strewn secondary peak (310 m) surmounts the eastern section of the hill (Fig 8).
- Mt Stirling comprises two offset elongate complex domes trending NE-SW (Figs 3 & 9) and connected by a slightly lower granite ridge. The base of the hill stands at 250-290 m asl, the crest of the west dome at 330 m plus, and the east dome at 370 m plus asl. A rock platform on the southern flank of the western dome stands at 290 to 300 m asl. The plan outlines of the residual are determined by steeply-dipping NE-SW fractures, within which sheet fractures and structures (Fig 5A) are developed. A-tents indicate expansion of up to 10% on compression and rupture. Flared basal slopes on the southern base of the eastern dome are associated with steeply dipping sheets and appear to have developed beneath talus accumulations. One sector of this slope appears to have been protected against basal sapping and weathering by stream diversion along fractures (Fig 10). Tafoni, rock basins and shallow gutters are widely developed and speleothems occur at suitable sites.
- Middle Dome is located between Mt Stirling and Gundaring Hill (Figs 3 & 9). As its name suggests it is a hemisphere or half-orange, smooth, devoid of soil and vegetation, and standing at about 300 m asl and 20 m above the level of the surrounding plain.
- Gundaring Hill and Tutakin Hill consist of two offset elongate (NE-SW) domes linked by a col (Fig 9). Tutakin Hill stands 300 to 360 m plus asl, and Gundaring Hill 270 to 370m asl plus and some 90 to 100 m higher than the adjacent plains and valleys. Kluftkarren, rock basins, A-tents, steeply dipping sheets and slipped slabs are represented as are large boulder tafoni with speleothems.

A



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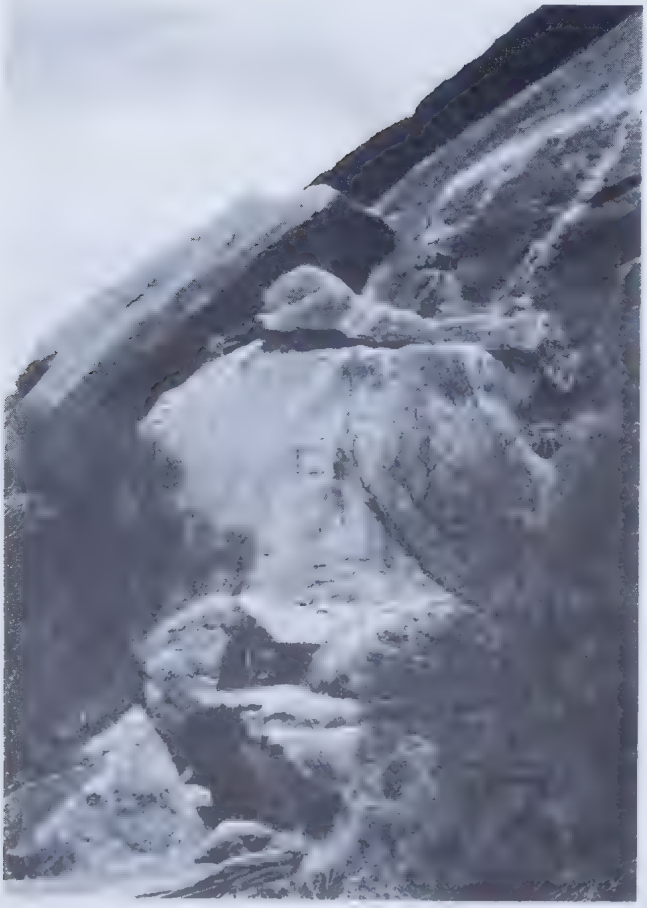

Figure 5. A: Sheet structures exposed in Mt Stirling. **B:** Slipped slab at Kokerbin Hill.

- Nangeen Hill is a boulder-strewn nubbin standing 270 to 310 m plus asl, and 40 m above adjacent plain.
- Kokerbin Hill (Fig 11) is a dome-on-dome structure with a shoulder at about 320 m asl and the crest at 360 m plus. The summit stands some 70 m higher than the surrounding plains. A minor boulder-strewn hill NNW of the main peak rises to more than 320 m plus. Basal flares and associated tafoni are prominent as are steeply dipping and slipped sheet structures (Fig 5A). Splitting and displacement of crystals along sheet structures indicates dislocation along sheet partings (Fig 12). Boulder tafoni, speleothems, A-tents (on lower slopes), tafoni with collapsed roofs (Fig 6), and chaotic masses of disturbed blocks and slabs also occur.

Origin of the Bornhardts

Why are bornhardts in general, and in particular those of the Salt River Valley, upstanding? Several hypotheses have been advanced in explanation of the residuals (for reviews, see Twidale 1982a,b; Vidal Romani & Twidale 1998). Many hypotheses have local validity, but the two proposed as general theories and most commonly cited involve scarp retreat and structural factors, and particularly fracture density.

According to the scarp retreat hypothesis (Fig 13A), bornhardts and other inselbergs are the last remnants remaining after long distance scarp retreat (Holmes 1918; King 1942, 1949; see also Ollier & Tuddenham 1962; Selby 1977). They ought therefore to be located on major divides and not in or near major river valleys. However, all but one of the most prominent residuals of the Salt River area occur close to the main channel and within the dissected fringe of the adjacent plains. Even Kokerbin Hill, which is some 6 km from the Salt River channel, although still within the zone of dissection, at its base stands only 70 m above river level.

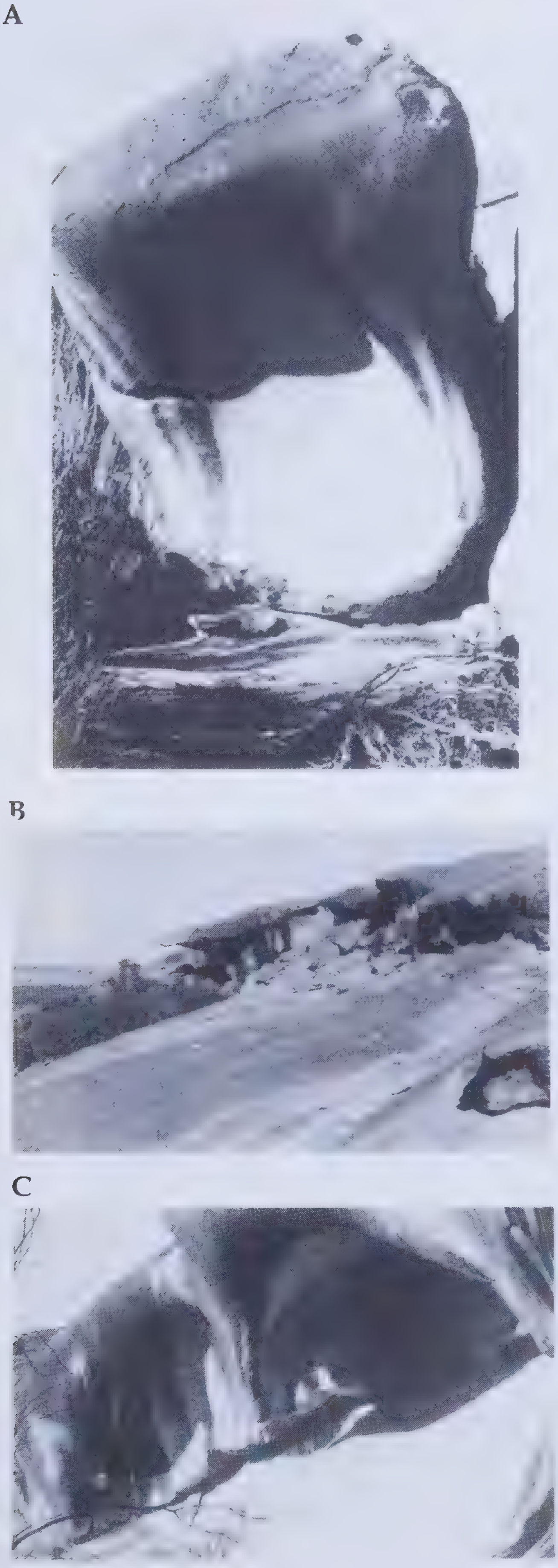

Figure 6. Kokerbin Hill: **A:** boulder tafone, **B:** tafone with collapsed roof, **C:** cliff-foot cave and flare.

The second widely accepted explanation of bornhardts is that they are structural forms developed on compartments of rock which are more resistant than the surrounding rock masses, and which withstand subsurface moisture attack (Fig 13B). The greater resistance of compartments may reflect either rock composition or fracture density (massive, low density or widely spaced partings). When base-level is lowered the weathered zones are evacuated and the bedrock surface - the erstwhile weathering front (Mabbutt 1961) - is exposed, with the resistant compartments upstanding. This two stage explanation was first advocated by Falconer (1911) and has since found widespread support both in the field and in the comparatively recent literature (*e.g.* Linton 1955; Wilhelmy 1958; Ollier 1960; Twidale 1964, 1982a; Thomas 1966; Godard 1977). Variations in structure most commonly take the form of contrasts in fracture density. These may be due either to folding producing antiforms and synforms, domes and basins (*e.g.* Lamego 1938; Myers & Watkins 1985), or shearing (Twidale 1980), in each instance leading to the development of compressive cores which develop into bornhardts.

Local evidence suggests that the Salt River Valley bornhardts have developed in this way. The regional pattern of palaeochannels is determined by gross fracture patterns (Salama 1997) dominated by NE-SW trends, although with prominent ENE-WSW and east-west elements (Figs 1 & 2). The Salt River valley sector south of Kellerberrin is aligned latitudinally and is, and viewed *in toto*, part of the regional pattern. Several of these bornhardts are largely defined by steeply dipping fractures amongst which NE-SW trends are prominent.

The Salt River Valley bornhardts are not the only massive compartments in the area. Low large-radius domes and platforms (most of them unnamed but some of them prominent and impressive) with bare granite exposed are found on the divides. Many are well exposed in the gently sloping sidewalls of the main valley as well as in shallow incised valleys eating back into the watersheds between the Salt and the Mortlock river systems, and in the main channel of the Salt River and various of its left bank tributaries (Fig 1). Their geometry and location suggest that several of these are at least as extensive and massive as Mt Stirling and the other Valley bornhardts, but whereas the latter have been exposed, or partly exposed, as a result of the incision of the Salt River, the others remain essentially concealed by the regolithic cover. Mt Stirling and the other bornhardts of the Salt River Valley are bornhardts because they happen to be located close to the major drainage line of the area.

In reality, the "two-stage" explanation is an over-simplication, for though weathering and erosion are the two prominent stages involved, both processes have exploited older, and in the Yilgarn Craton, much older, structural weaknesses such as fractures in the country rock. The mechanism is really multi-stage for the development of the regional fracture pattern, probably in earliest Proterozoic times, must be taken into account (Twidale & Vidal Romani 1994), but for the sake of brevity the term "two-stage" is retained here.

In the Salt River Valley the residuals are all developed in an Archaean seriate adamellite, which bedrock

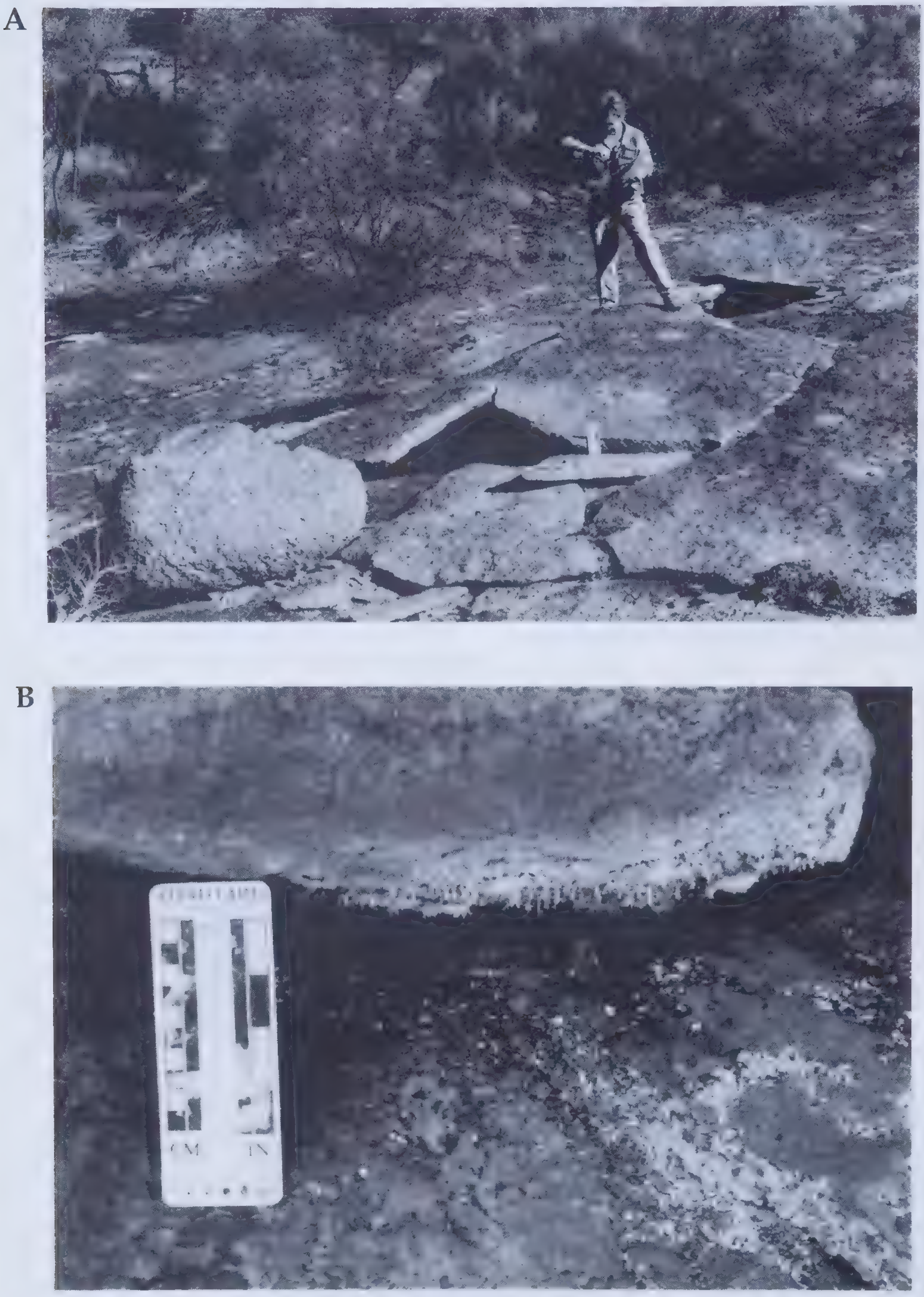

Figure 7. A: A-tent at Kokerbin Hill. **B:** Siliceous speleothems (stalactites). Each stem is of opal-A, with a tip of gypsum.

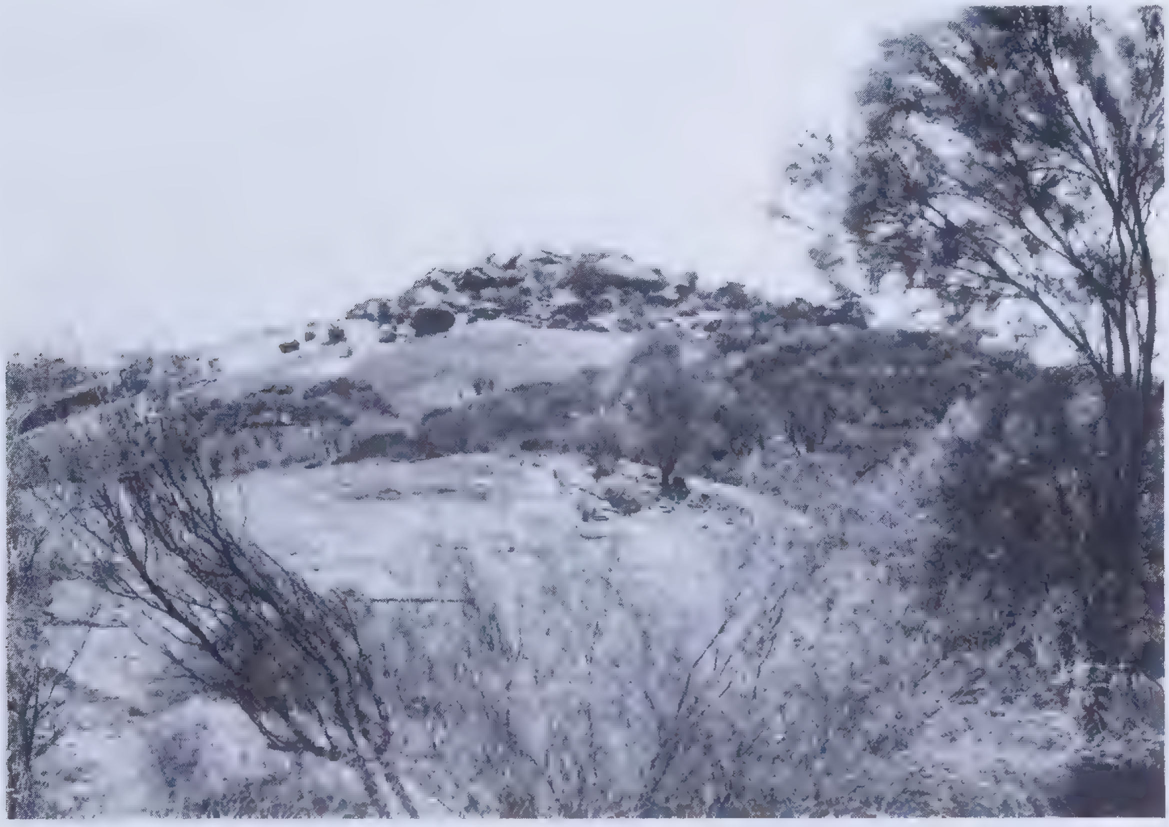

Figure 8. The eastern peak of Mt Caroline, showing boulder- and block-strewn crest.

appears both in hill crests and in lower slopes. Variations in fracture density are suggested by the massiveness (scarcity of open fractures in the residuals) compared with the close jointing and mildly weathered granite exposed in some road cuttings and borrow pits at lower elevations in tributary valleys. According to some interpretations sheet fractures on the one hand (Twidale 1964; Vidal Romani *et al.* 1995) and A-tents on the other (Twidale & Sved 1978; Wallach *et al.* 1993) can both be taken as indicating past or continued shearing. The en echelon pattern of Mt Stirling and Gundaring-Tutakin hills is also suggestive, as are the offsets discernible in the distribution of fractures implied by straight channel sectors (Salama 1997; Figs 2 & 9).

Age of the Landforms

General Remarks

In describing the age of a land surface or a landform, geomorphologists use the same convention as geologists and winemakers. Just as a basalt flow which was extruded some 60 Ma in the Eocene and which persists in the landscape is referred to according to its age of initiation, and just as a wine is referred to in terms of the year in which the grapes from which it is derived were harvested, so the age of a landform refers to the date of initiation. In reality, of course, few landforms develop instantaneously; a fault scarp, for example, may, but most landforms evolve over time, so that they have an age-range. However, this characteristic is accommodated in the immensity of time. Just as the basalt earlier referred to is altered in time and the wine matures (or deteriorates), so also do landforms not go unchanged; but all are still labelled according to date of initiation.

Ayers Rock (Uluru), for example, is a domical hill or bornhardt with a prominent bevelled crest, eroded in steeply dipping Cambrian sandstone which stands in isolation in the desert landscapes of central Australia. The summit bevel is an etch surface for it is devoid of soil or regolith. Local stratigraphy suggests it was formed as part of a weathering front in the latest Cretaceous (about 70 Ma) and that it was exposed during the Early Cainozoic, for Oligocene lake beds occur on the plains around the residual. The steep slopes that flank the bevelled summit are much younger, and are due to successive (at least two) phases of scarp-foot weathering and erosion during the Cainozoic.

Salt River Valley

In the Salt River landscape, too, the bornhardts are two-stage forms. They originated as bedrock projections on the weathering front beneath a lateritised land surface during the Cretaceous (and possibly also in earlier Mesozoic times), but were first exposed as domical landforms during the Cainozoic. They may be as old as the Eocene but were definitely exposed by the Miocene, when the Salt River had eroded a considerably deep valley in the adjacent valley floor. The exposure may have been gradual, but it more likely occurred in stages or phases - there are suggestive benches at 290 to 300 m asl and 30 to 40 m above plain level on Mt Stirling (*cf* Twidale & Bourne 1975) - with pauses during which there was scarp-foot weathering.

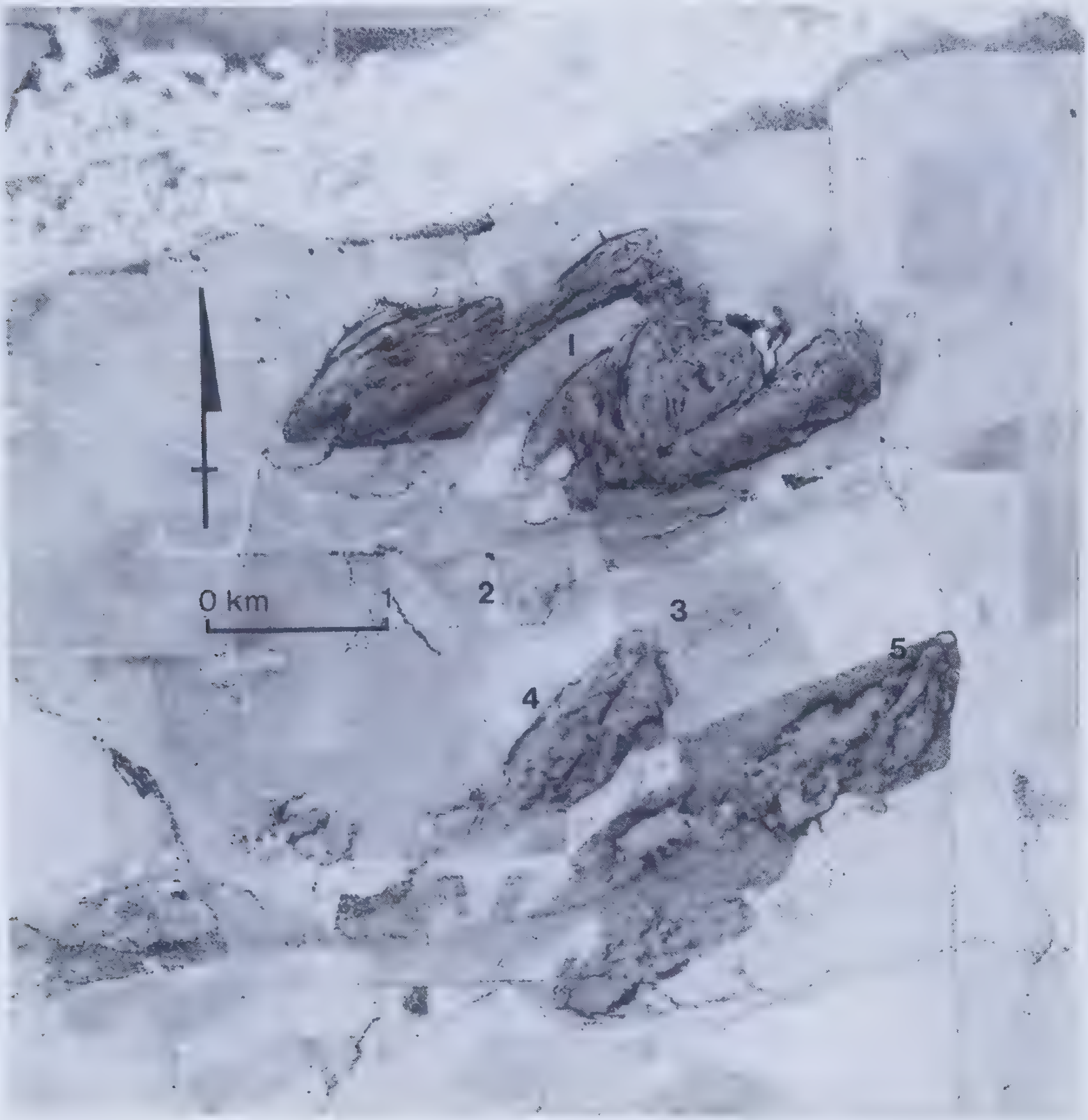

Figure 9. Extract of vertical air photograph of part of Salt River Valley south of Kellerberrin, showing granitic residuals (1: Mt Stirling, 2: Middle Dome, 3: minor nubbin, 4: Gundaring Hill, 5: Tutakin Hill) and in particular the fracture-defined *en echelon* structural and topographic patterns exposed in Mt Stirling and Tutakin and Gundaring hills. (WA 1428 Kellerberrin sheet, Run 15, Frame 5238, 16.11.72. Reproduced by permission of DOLA, Perth, Western Australia).

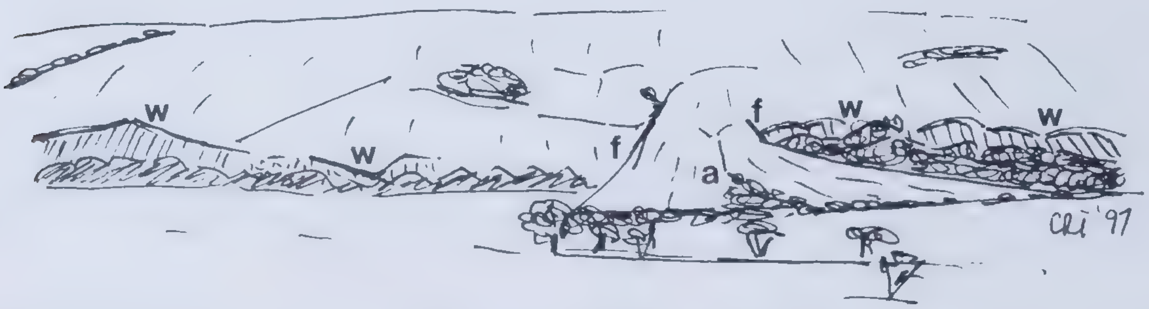

Figure 10. Sketch of part of the southern slopes of Mt Stirling showing protected apron. a: apron, f: fractures into which runoff diverted, w: upper limit of former talus slope and associated subsurface weathering.

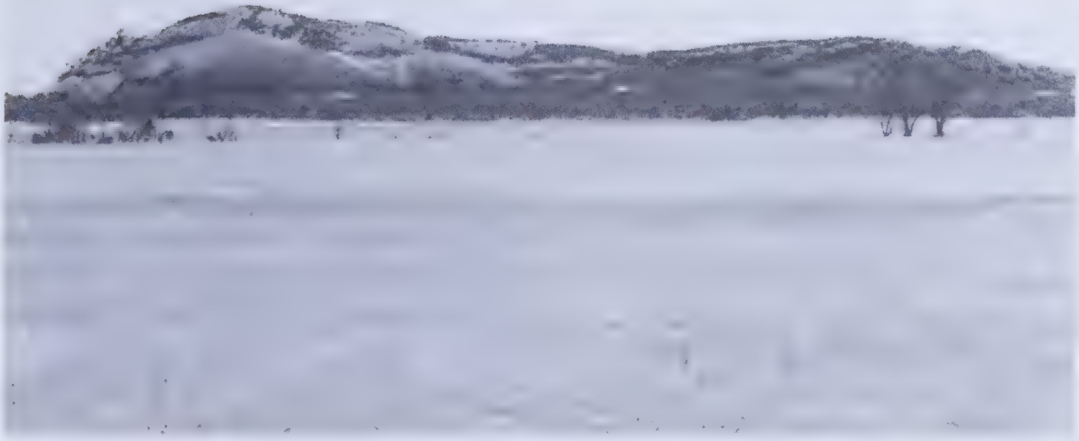

Figure 11. General view of Kokerbin Hill from the east, showing dome-on-dome morphology.

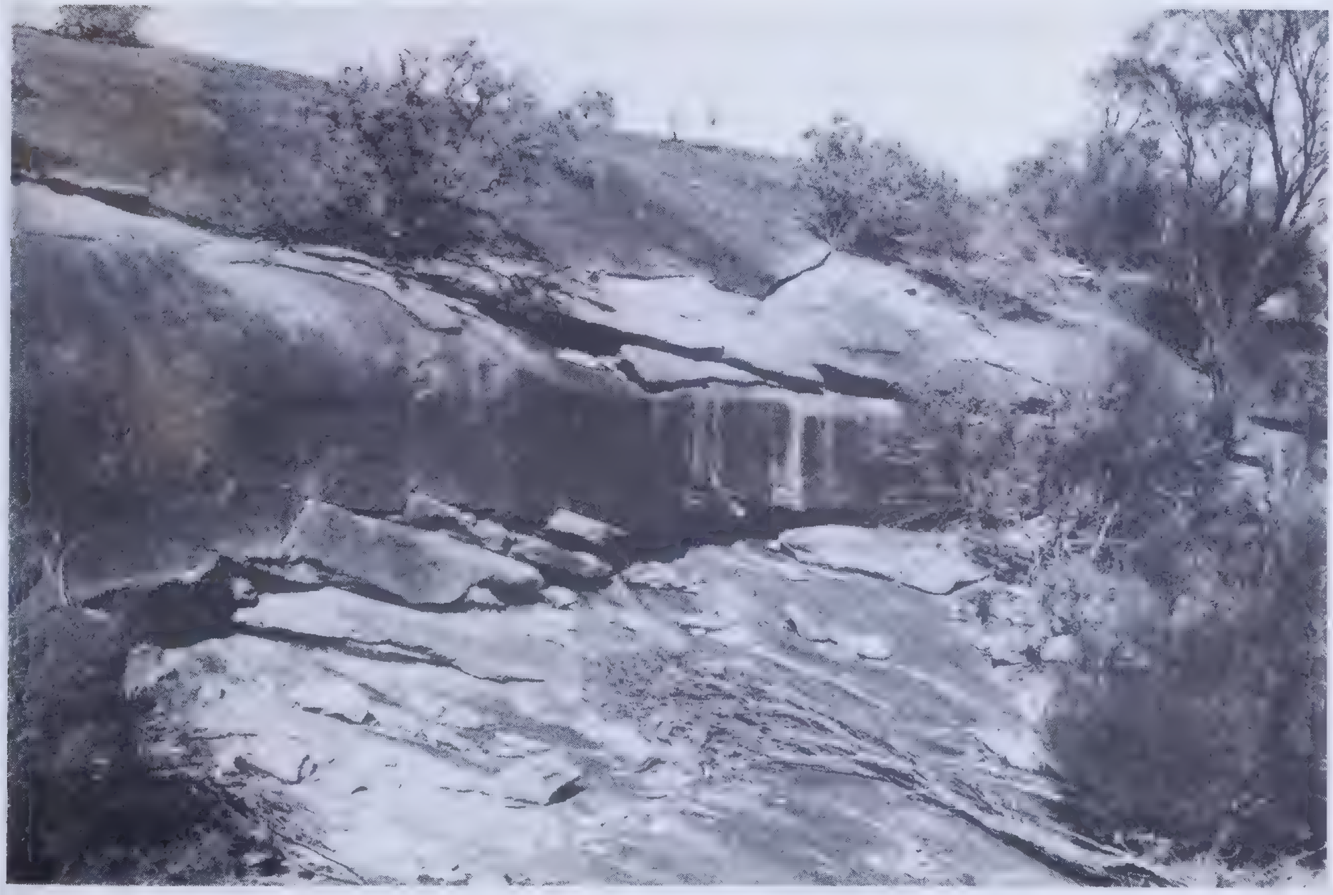

Figure 12. Sheet fractures at Kokerbin Hill. Crystals located on opposite sides of the partings are split and demonstrably displaced.

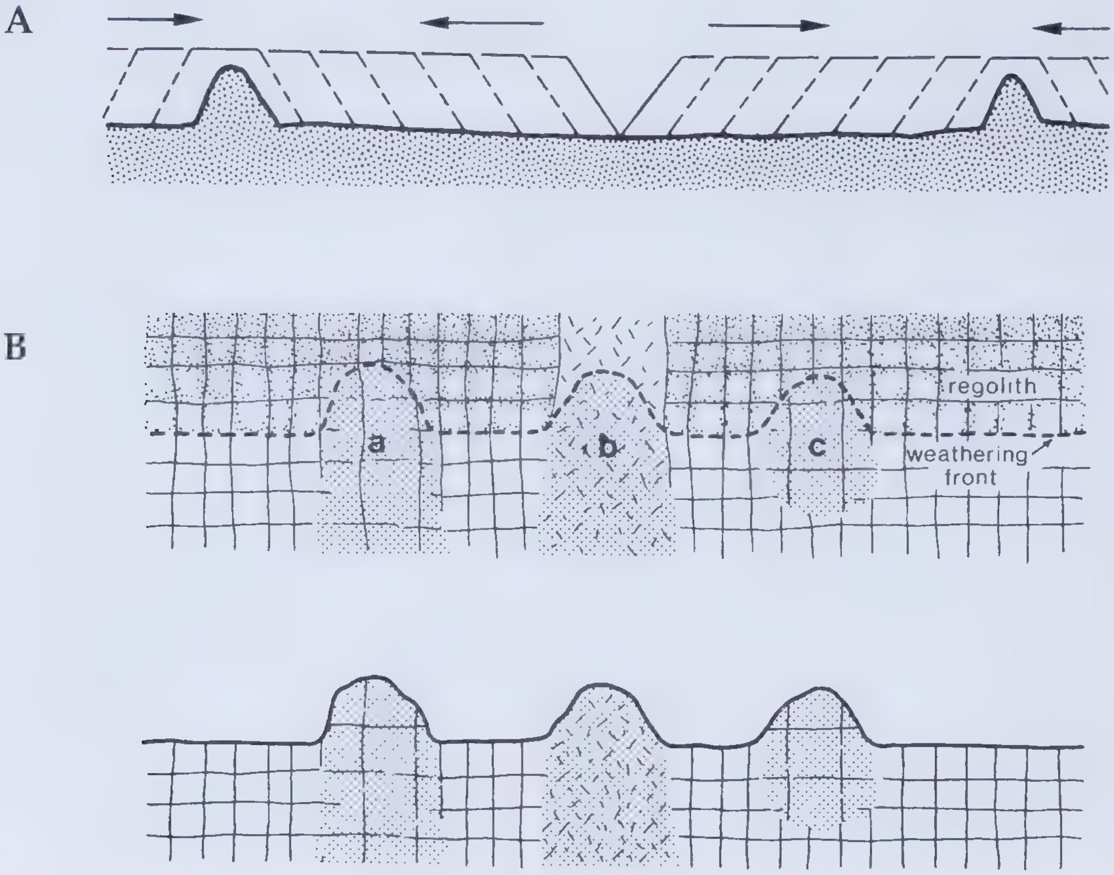

Figure 13. A: Inselbergs/bornhardts due to scarp retreat (modified from King 1942, 1949). **B:** The two-stage model of inselberg/bornhardt development. a: column of massive rock (few fractures), b: discrete mass of massive rock, c: more resistant rock type. (modified from Falconer 1911)

Another deducible consequence is that in terms of the scarp retreat hypothesis, no residual remnant ought to be older than the duration of a cycle, which, for a large land mass, is of the order of 33 Ma (Schumm 1963; Twidale 1982a). In stratigraphic terms, no bornhardt ought to be older than Oligocene. Many bornhardts (excluding those many exhumed forms) are demonstrably older than this supposed limit. Ayers Rock and The Olgas for instance are of the order of 70 Ma (Twidale 1978; Harris & Twidale 1991) and residuals like The Humps, King Rocks and Jilakin Rock to the southeast of the Salt River Valley, and Ulonging Hill, to the south, are at least of Cretaceous age (Twidale & Bourne 1998).

The age of the Salt River forms can be inferred from their relationship with the lateritised land surface which can in turn be inferred from its relationship with river channels and associated deposits of known age. The weathered (lateritised) land surface of Jutson's (1914) Old Plateau was shaped by rivers graded to these trunk streams. The incision of this drainage system caused the rejuvenation of the tributaries and the stripping of the regolith to expose not only the high plain of Jutson's New Plateau, but also many bornhardts such as Hyden Rock (Twidale & Bourne 1998). Stratigraphic evidence from many palaeochannels in the southern Yilgarn Craton shows that some of the bedrock valleys were incised by the Eocene, for alluvial fills of that age are widely distributed (Commander 1989; Kern & Commander 1993; Clarke 1994; Waterhouse *et al.* 1995) though Miocene and Pliocene fills are also well known (*e.g.* Salama 1997). Presumably incision was not instantaneous along the length of any major river but took considerable time to regress headwards (see also Taylor *et al.* 1985). Given the age of the river rejuvenation it seems likely that it was caused by tectonism related to the separation of the Australian and Antarctic plates, and in particular the uplift and northward tilting of the southern edge of the Yilgarn Craton.

The Salt River Valley is a palaeochannel of at least Miocene age (Salama 1997; Fig 14). A river has probably occupied the present sector since the Early Tertiary. Uplift of the Darling Range blocked the previous drainage, and caused the formation of a shallow lake but rejuvenation and regression of the Avon has drained the lake (of which only minor remnants remain) and revived the Salt River system, so that the palaeochannel cut some 70 m into the granitic country rock before being infilled to its present level. Thus the local evidence derived from the demonstrated minimum age of the river channel points to river incision prior to the Miocene. It was in this phase of incision that tributaries to the Salt River were regraded and the divides to either side of the channel dissected. It was then that Mt Stirling and the other bornhardts were exposed. This is a minimum age, for the regional evidence suggests an Early, rather than a Middle,

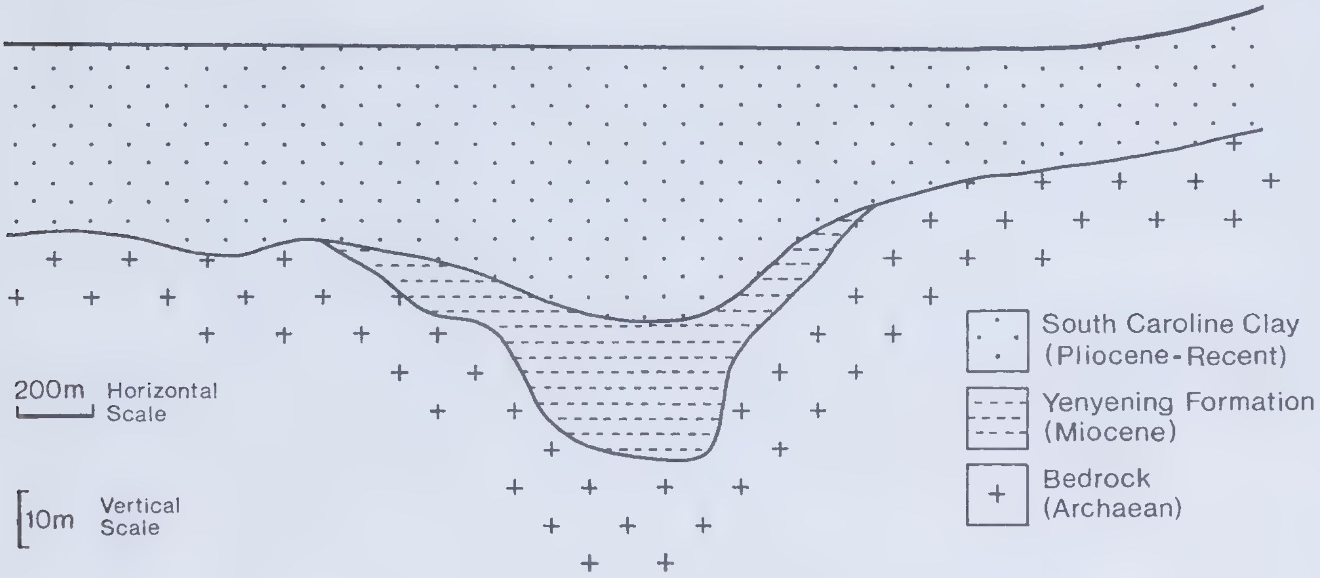
200m Horizontal Scale
10m Vertical Scale
South Caroline Clay (Pliocene-Recent)
Yenyening Formation (Miocene)
Bedrock (Archaean)

Figure 14. Section through the Salt River showing buried basement channel and fills. The Yenyening Formation consists of clay, sand and lignite (simplified from Salama 1997)

Tertiary age for the drainage system and this part of the Salt River Valley may have been eroded much earlier in the Tertiary, but alluviated during the Miocene.

Other explanations for bornhardt formation which are, *prima facie*, relevant include the suggestion that bornhardts may be developed on intrusive stocks which are, implicitly, different and more resistant (composition, texture, fracture density) than the host masses. In the Salt River Valley there is no evidence that the rocks in which the bornhardts are shaped are compositionally or texturally different from plains rocks, though there are compositional and textural variations within many of the bornhardts.

Mt Stirling, Gundaring Hill, Tutakin Hill, Kokerbin Hill and Mt Caroline are domes, the bevelled crests and shoulders of which originated as a result of weathering in the zone of fluctuating water table in Cretaceous times (Fig 15). The ancestral massive compartment that was to become Nangeen Hill was entirely below the surface and its outer layers were reduced to regolith, and blocks and boulders within the regolith, so that on exposure it appeared as a nubbin. Middle Dome was similarly wholly hidden beneath the regolith and its concentric outer sectors, or shells, were so weathered that soon after exposure they were eliminated to leave the hemispherical core as a rounded hill.

On Mt Stirling, Tutakin Hill and Mt Caroline there are small protuberances or knolls standing higher than the crestal bevel or shoulder. Given their present elevations, those of the adjacent watersheds and the known local thickness of the lateritic regolith, they were most likely exposed above the laterite surface. Alternatively, if the regolith thickened in the valley, or present elevations are misleading due to tilting, they may have been irregularities projecting into the base of the regolith (Fig 14). On Kokerbin Hill, the shoulder or break of slope between the two domes probably denotes the level of the regolith and the higher or summit dome may well have been a low hill projecting above the lateritised land surface in later Cretaceous-early Eocene times. Certainly the higher dome (above the level of the car park) is intensely weathered, with many shelters and tafoni developed beneath large residual boulders and sheet structures (Fig 6A,B).

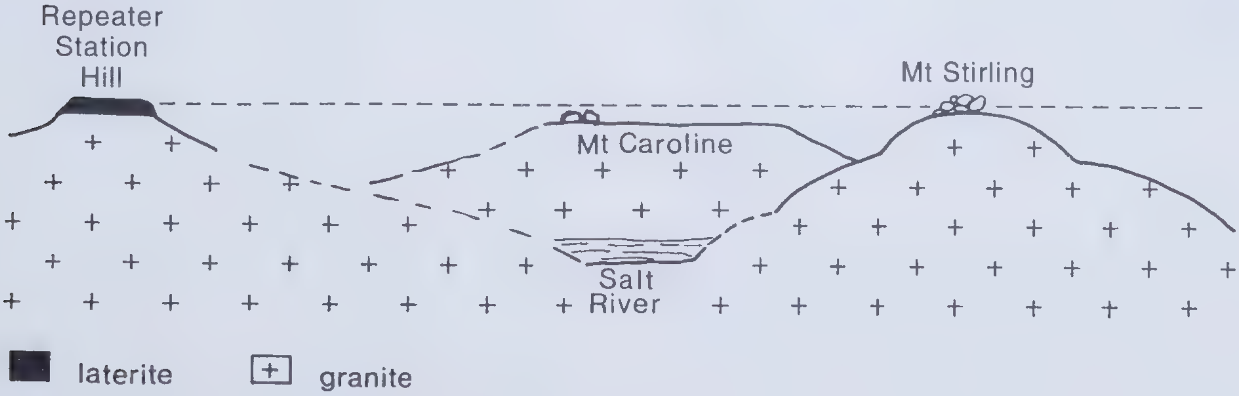

Figure 15. Diagrammatic section of the Salt River Valley showing location of residuals in relation to weathering surface.

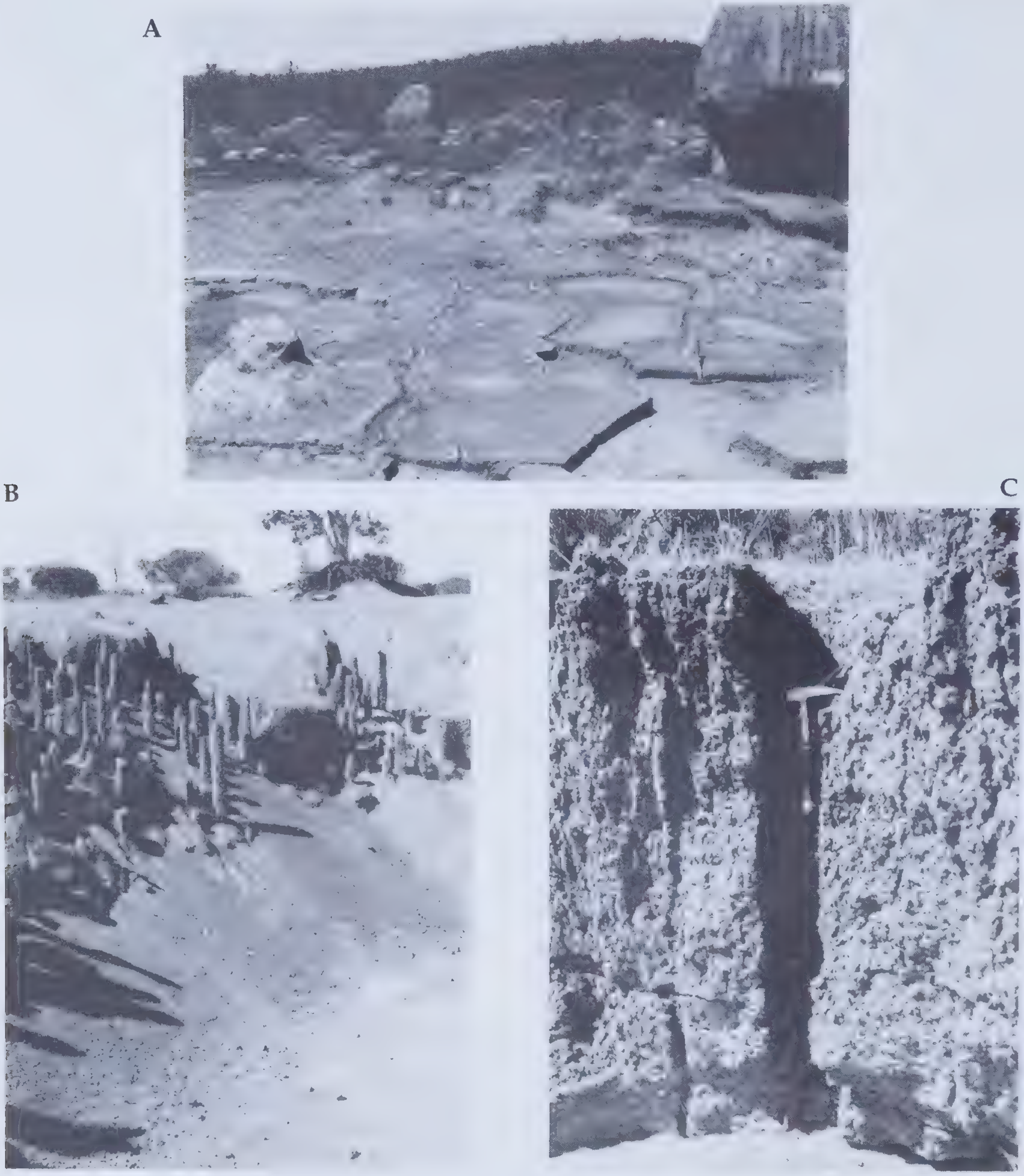

Figure 16. **A:** Tesselated pavement at Boulder Rock. **B:** Two metre high pinnacles of pisolitic iron oxide cemented by kaolinite near Ulonging H S. **C:** Pipes in pisolitic zone of laterite at Repeater Hill.

Thus the Salt River Valley residuals are typical two-stage forms, with two major ages. The first relates to the period in the Cretaceous (and possibly also in earlier Mesozoic times, including the Triassic and Jurassic) when they were prepared by differential moisture weathering in the subsurface, which exploited varied fracture densities in the bedrock. The second pertains to the period of exposure resulting from the incision of the Salt River and its tributaries. There is, however, the possibility that minor precursors of several of the present forms were already standing in relief above the lateritised land surface in the Cretaceous. In this they are analagous to various other very old residuals of the region, bornhardts such as The Humps, King Rocks, Jilakin Rock and the upper dome of Boyagin Rock (Twidale & Bourne 1998).

Iron Impregnation and Tesselated Pavement

If, as is suggested, the bornhardts of the Salt River Valley evolved beneath a lateritised weathered land surface, *i.e.* one in which iron oxides such as haematite and goethite were concentrated in the B-horizon, then it is strange that ferruginous staining and associated effects are not more prominent on the bornhardts. At Boulder Rock, in the Darling Ranges, about 20 km east of Kelmscott, however, iron staining of the surface is preserved and a tesselated pavement in granite (Fig 16A) is also developed. Iron oxides have evidently percolated down vertical fractures and indurated the adjacent parts of each small slab, leading to the formation of raised rims enclosing a shallow depression in each component of the pavement. Some iron salts, however, have been contributed in dust blown to the site by easterly winds (Glassford & Semeniuk 1990; Brimhall *et al.* 1991).

Similarly tesselated granite surfaces have been observed on the lower slopes of Domboshawa, a bornhardt located a few kilometres northeast of Harare, in Zimbabwe. There the patterns clearly developed at the weathering front, beneath a thin regolith carrying a cover of mosses and small shrubs.

Eucalypts spread over the Australian continent and became dominant beginning in the Miocene. Waters containing polyphenols, which are produced by eucalypt litter, are especially effective in dissolving iron-rich materials (see Bloomfield 1957), so that there has been ample time for iron oxides to be translocated from lateritic profiles into the deeper regolith and to the weathering front. However Boulder Rock has, in geological terms, and in comparison with the Salt River residuals (and others in the southern Yilgarn), only recently been exposed; remnants of the deeply weathered land surface occur extensively in the Darling Ranges and in its eastern dissected margin. Perhaps there has not yet been time for the ferruginous minerals precipitated at and near the weathering front to be leached from the system by meteoric waters. To the east, on the other hand, remnants like those in the Salt River Valley have been longer exposed to the elements so that despite the lower average precipitation there has been more opportunity to wash away iron concentrations, except at minor, exceptional sites, such as iron oxide-capped spikes on the eastern dome of Hyden Rock. In addition, alkaline groundwaters and runoff may here, as elsewhere, be especially effective solutional (weathering) agents.

Pisolitic Pinnacles

The piped structure of the ferruginous carapace exposed at Repeater Hill is germane to the origin of pinnacles of pisolitic zone laterite (Fig 16B,C) developed near Ulonging H S (Althorpe Peaks), some 18 km ESE of Quairading and 30 km SSW of the Salt Creek area. The pinnacles are exposed in a borrow pit and rise about 2 m from a debris slope composed of disintegrated pisolitic detritus. They are cemented by kaolinite and stand about a metre below the level of the original laterite surface preserved, for example, around trees. Circular patterns with white and red clay filling interstices in the adjacent floor of the pit suggest that pinnacle structures were formerly (before quarrying) more extensive. Moreover the occurrence of round patches of white clay with pisolites shows that associated structures extend an unknown distance in depth, below the floor of the quarry. They could have originated as infillings of pipes such as those exposed at Repeater Hill, where the A-horizon, which is composed overwhelmingly of quartz, nevertheless contains minor amounts of kaolinite, feldspar and chlorite. Thus the Ulonging pinnacles are pipe fills of detrital pisolites cemented by clay. They occur in a pisolitic zone and stand lower than the original surface and sandy A-horizon. They are not, however, due to solution but to flushing of fines and partial infilling by clay (Twidale & Milnes 1983; Glassford 1987; Herwitz & Muhs 1995).

Conclusions

The area south of Kellerberrin includes, first, remnants of the weathered (lateritised) land surface that is widely preserved in the southern Yilgarn Craton, and the age of which can be deduced; second, a sector of the Salt River Valley the origin and age of which has been determined; and third, several prominent granitic bornhardts. This assemblage of landforms allows the origin and age of the bornhardts to be suggested.

The bornhardts are multi-stage forms due to differential weathering along fracture sets and systems initiated more than two billion years earlier. They were prepared by subsurface weathering during the Cretaceous, and possibly earlier Mesozoic times, and exposed as landforms during the Tertiary, certainly during the Miocene, although probably from the Eocene onwards. The crestal domes and minor nubbins present on the higher residuals may have stood above the lateritised landscape and be similar in age to several other of the older Yilgarn bornhardts. The lateritic carapace has affected minor landform development at Boulder Rock, and piping in the duricrust has resulted in pinnacles in the piedmont of Althorpe Peaks.

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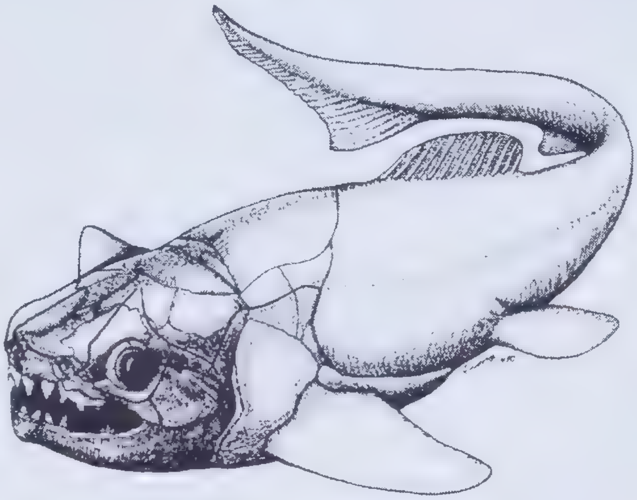
GOGO FISH

(*Mcnamaraspis kaprios* Long, 1995)

Fossil Emblem of the State of Western Australia



[drawing by John Long]

In the far north of Western Australia, about 100 kilometres south-east of Fitzroy Crossing, are the remains of a giant barrier reef that 370 million years ago teemed with life. From shales known as the Gogo Formation, that formed in quiet inter-reef bays have come exquisitely preserved, three-dimensional skeletons of the fishes that swam in these ancient seas. Preserved as original bone in limestone nodules within the shale, they represent the best preserved early fishes in the world.

One of the major groups of extinct fishes that swam around these ancient reefs is a group known as placoderms. One is *Mcnamaraspis kaprios*, a fish that in life would have been about 25 centimetres long. Like other placoderms, it is characterized by a bony head shield which articulates in a ball-and-socket joint to a trunk shield. In life it possessed a shark-like body, with a single dorsal fin, fleshy paired pectoral and pelvic fins; and an anal fin.

Mcnamaraspis is special in that the fossils have annular cartilage preserved in the snout, the first evidence for this structure in placoderm fishes. This is significant because it demonstrates a close evolutionary relationship between sharks and placoderms. This, combined with the sharp, prominent teeth, imply that *Mcnamaraspis* was a voracious predator, probably feeding on the small, shrimp-like crustaceans that abounded in the warm. tropical seas of prehistoric Western Australia.

Mcnamaraspis kaprios was found by Dr John Long in August 1986 and described by him in 1995. It was declared the fossil emblem of the State of Western Australia by His Excellency Major General Philip Michael Jeffery, Officer of the Order of Australia, Military Cross, Governor of the State of Western Australia, on 5 December, 1995.

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[John Long, Western Australian Museum]

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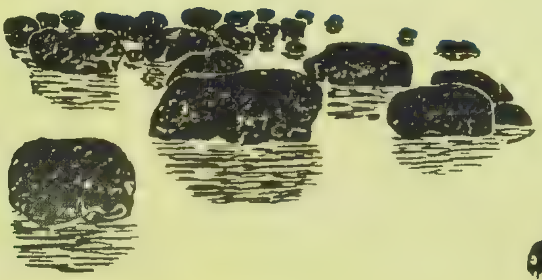

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The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor) and the Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance

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Abstract

Ocean currents operating near the reef front at Ningaloo were studied by direct observation, aerial surveys (1990-92), and a current drogue, demonstrating a predominent northward current along the reef front during late summer and early autumn. It is proposed that this current be termed the "Ningaloo Current". Satellite sea surface temperature images show that this Ningaloo current is in fact the dominant current on the inner shelf from September to mid-April each year, and is a counter-current to the southward Leeuwin Current further offshore at the shelf break. The satellite imagery and current drogue data demonstrated how these opposing currents generate a recirculation of water in the region. The Ningaloo counter-current may determine the dispersal of coral larvae following the autumnal mass reef spawning. The circulatory movement may also be important in retaining planktonic biomass within the Ningaloo ecosystem, and is probably responsible for the extremely active food chain at this time of year and the presence of whale sharks. It may also, through natural selection, influence the timing of spawning of corals and other invertebrates on the reef.

Introduction

The dominant current off the west coast of continents throughout the world is an equatorward cold current forming the eastern limb of the subtropical gyres. In the south-eastern Indian Ocean, this current is generally depicted as a cool West Australian Current flowing northwards, but it is now known that the boundary current off Western Australia is in fact the warm poleward-flowing Leeuwin Current (Cresswell & Golding 1980; Godfrey & Ridgway 1985; Pearce 1991).

The Leeuwin Current is a stream of low salinity, warm tropical water that maintains the waters of the west coast of Australia at temperatures suitable for coral growth, and is thought to help sustain the extensive coral reefs that are found at Ningaloo Reef and the Houtman Abrolhos Islands about 29 °C (Hatcher 1991). It flows most strongly during the autumn, winter and early spring months, and has an important influence on many biological processes along the coast (Cresswell 1991; Phillips *et al.* 1991; Hutchins 1991; Hutchins & Pearce 1994). Both satellite imagery (A F Pearce, CSIRO Marine Research, Perth, unpublished data) and ship-borne observations (Thompson 1984) indicate that the Leeuwin Current is often narrow and comparatively close to shore off the Ningaloo Reef where the continental shelf is very narrow (Fig 1).

Ningaloo Reef stretches some 260 km south from North-West Cape (Fig 1), and is the only extensive coral reef in the world fringing the west coast of a continent. The distance offshore averages only 2.5 km, varying from only about 200 m to 7 km (R F May, National Parks

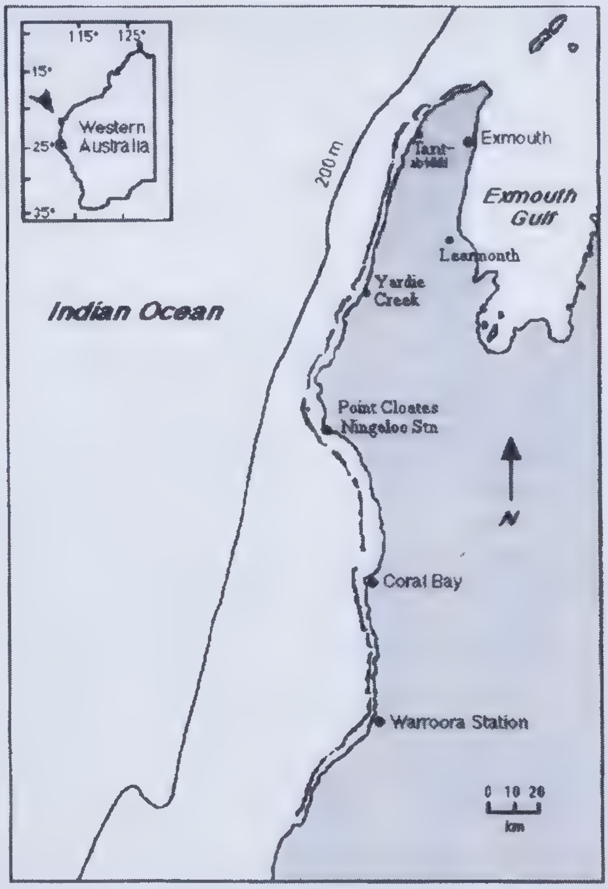

Figure 1. The Ningaloo Reef stretches 260 km along the west coast of the North-West Cape. The location in Western Australia is shown (inset). The dashed line indicates the approximate position of the 200 m. contour, on the edge of the Continental shelf.

Authority, personal communication) and partially enclosing a coastal lagoon between 1 and 2.5 m deep at low spring tide. Hearn & Parker (1988) have estimated that the gaps in the northern portion of the reef comprise some 15% of the length.

The continental shelf break in the northern reef at Ningaloo is at a depth of about 100 m and is only 6 to 10 km offshore; this is the narrowest part of the shelf in Australia. The coastline veers sharply eastwards, south of Point Cloates (Fig 1), and the width of the shelf (100 m contour) increases to over 30 km. On this wider shelf, the shelf break is not very strongly defined compared to further north where a number of steeply shelving underwater canyons are a feature.

Studies of the lagoon sea temperature and tide in the Ningaloo reef system (Simpson & Masini 1986) showed that the tides were semi-diurnal, with spring and neap tides occurring 2-4 days and 8-10 days respectively after a full or new moon. They found considerable diel variation in temperature, the range averaging 3 °C. There was a good correlation between measured temperatures and those determined by satellite imagery. Occasional temperature anomalies were noted, involving a sharp drop in temperature of 1 to 2 °C below seasonal values for 2 to 3 days, usually during neap tides.

In an extensive review of oceanographic processes in this area, Hearn *et al.* (1986) explored various scenarios that might cause these temperature anomalies, the arrival of a body of colder water, upwelling off the Ningaloo Reef, or large internal waves. They concluded that the fall in temperature is probably caused by upwelling associated with internal wave activity. Measurements of the circulation across and around the reefs indicated that water transported shorewards across the reef by wave and swell action tends to flow along the lagoon and out at the ends (mainly towards the south). The residence time of water within the lagoon system is a matter of hours (Hearn & Parker 1988).

Water circulation on fringing reefs has been extensively studied in Guam (Marsh *et al.* 1981). Under normal conditions, water entering the lagoon over the reef finds its way to adjacent gaps where it flows back out to the ocean. The flow in the gaps only reverses in conditions of a strong rising tide. Observations at Ningaloo show a similar current system (Hearn *et al.* 1986).

Studies further south along the Western Australian coast have demonstrated that there are inshore, wind-driven, northward counter-currents to the Leeuwin current near the Abrolhos Islands (29° S; Cresswell *et al.* 1989; Pearce 1997) as well as between Cape Leeuwin and Cape Naturaliste (34° S) from November to March each year (Pearce & Pattiaratchi 1999).

The scleractinian corals of the west coast of Australia reproduce each year in mass spawning events following the March and April full moons (Simpson 1985, 1991; Simpson & Masini 1986). The coral planula takes over 7 days to develop to a stage where settlement may occur and is dispersed by ocean currents. Theories regarding coral spawn dispersal at Ningaloo have hitherto assumed that spawn is dispersed southwards by the Leeuwin Current, which intensifies at this time of year. A unidirectional gene flow between separate coral reefs in Western Australia has been proposed (Simpson 1991).

We describe here surface currents on the continental shelf off Ningaloo between 1987 and 1992 using direct observation of current plumes, from boats, and aerial surveys (conducted for whale sharks, 1990 to 1992) and data from a current drogue. Confirmatory data were derived from satellite imagery (1991 to 1996) to confirm the existence of a seasonal inshore northwards counter-current.

Methods

No contemporary weather records for the Ningaloo Reef are available; the nearest station at Learmonth (Fig 1) is in the wind shadow of the Cape Range and therefore has somewhat different conditions from the west coast. Monthly wind rose data from a discontinued weather station at Cape Cuvier (24° S, immediately to the south of Ningaloo Reef) have been analysed to show seasonal variations in wind strength and direction.

Coral spawning events were personally observed on many occasions from boats at Bundegi Reef (north of the Exmouth township) in Exmouth Gulf and at Tantabiddi Reef and Coral Bay on the west coast (Fig 1). These data were supplemented with observations made by other divers, from other locations whenever possible (Table 1).

Table 1

Dates of confirmed coral spawnings, 1984 to 1996.

YEAR	MARCH	APRIL	COMMENTS
1984	25-26		Simpson (1985)
1985	15-16		Simpson (1985)
1986	3-4		
1987	21-23 *		
1988	10-12 *	9-10 *	
1989	29-30 *		
1990	18-19 *		
1991	9-10 *	7-8 *	
1992	26-27 *	24-25 *	
1993	16-17	15 *	
1994		3-4 *	
1995	25-26		
1996	14-15	10-13	Cyclone Olivia

* denotes spawning events directly observed by the authors; all other events verified by divers monitoring spawning at Exmouth and Coral Bay.

Preliminary direct observations of currents along the reef commenced in 1987. Although most of the water transport in the lagoons is parallel to the reef front (Hearn & Parker 1988), turbid water flows out of the lagoon through the major gaps in the reef and turns in the direction of the prevailing alongshore current. The boundary between the turbid lagoon water and the clear water offshore of the reef front can be clearly seen from boats and particularly from planes overhead, often extending over 500 m offshore (Fig 2). This phenomenon allows determination of the reef front current direction both from surface vessels and from aircraft.

Between 1990 and 1992, regular aerial surveys for whale sharks were conducted along the Ningaloo Reef from February to May using a single-engined Cessna

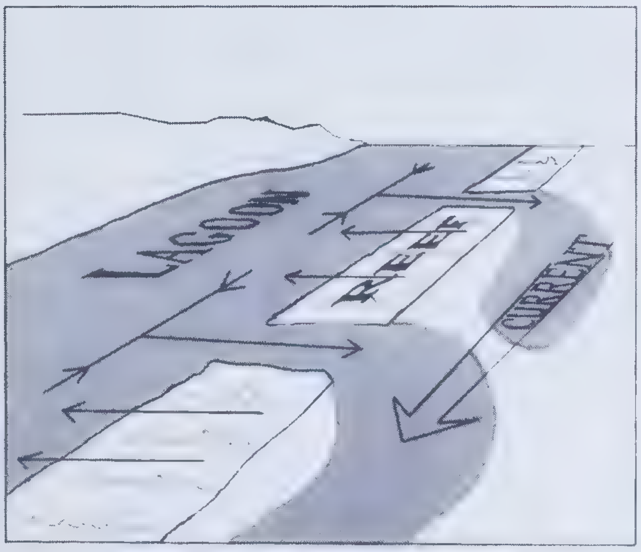

Figure 2. The Ningaloo Reef is a classic fringing reef, with a shallow lagoon. Surf coming over the reef brings a torrent of richly oxygenated water into the lagoon which returns to the open ocean via gaps in the reef. This turbid green-coloured water flowing through gaps in the reef can clearly be seen, particularly from the air. It is taken north or south along the reef front by the prevailing reef front current.

aircraft flying over the reef at a height of 370 m. For the purpose of assessing the prevailing current, the reef was divided into three sections (Fig 1); Tantabiddi to Yardie Creek, Yardie Creek to Point Cloates (Ningaloo Station), and Point Cloates to Coral Bay (this third section was only surveyed in 1991). The surveys were at about weekly intervals between February and May (Table 2). They were more intensive in 1991 with both morning and afternoon observations; in 1990 and 1992 extra flights were conducted.

On 11 April 1991, a Platform Transmitter Terminal (PTT) for satellite tracking utilising the ARGOS system, became detached from a whale shark off Tantabiddi at the northern end of the reef. This unit, which had a keel extending 30 cm below the sea surface, effectively became a current drogue, giving additional information about the prevailing current. Current measurements using current meters on the outer continental shelf (Boland *et al.* 1988, D R Tippins & M Tomczak, Flinders Institute of Atmospheric and Marine Sciences, unpublished data, personal communication) are also reviewed to show the larger-scale circulation features in the Ningaloo area.

Sea-surface temperature (SST) images of the area were obtained from the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA satellites. These enable circulation patterns in the water to be inferred when there are water masses (currents) with different temperatures. For overhead passes, the pixel resolution is about 1 km, so features less than about 2 km from the coast cannot be assessed; because the satellite precesses daily, for part of the time Ningaloo is near the edge of the pass where the spatial resolution is of the order of 5 or 6 km. In 1991 water temperature measurements were available from a thermistor on board the vessel "Nordon" operating outside the northern reef from early March until the middle of April, allowing confirmation of the satellite-derived sea surface temperatures.

Table 2

Current observations from the aerial surveys. The wind and current direction was determined from observations on aerial surveys. A "-" denotes that no current was detectable, usually because of insufficient flow from the lagoon. Wind directions are (by tradition) *from* and current directions are *to*.

1990

Date	Wind Direction	Current direction
05-Feb	S	-
10-Mar	SW	-
16-Mar	S	S
20-Mar*	SW	N
26-Mar*	SW	N
28-Mar	SW	S
02-Apr	SW	N
10-Apr	S	S
16-Apr	N	S
14-May	SW	S

In 1990 aerial surveys were flown from the northern end of the Ningaloo tract as far as Fraser island off Ningaloo Station. Take-off was usually at 14:00. Two additional flights along the reef produced current data, on 20 March at 10:30 and on 26 March at 17:00 (*)

1991

Date	Wind Direction	Current direction (3 sectors)		
10 Feb pm	SW	-	N	-
28 Feb pm	SW	S	S	S
06 Mar pm	SW	N	N	N
14 Mar am	S	-	-	-
14 Mar pm	SW	-	-	-
20 Mar am	SW	-	-	-
20 Mar pm	SW	-	N	-
28 Mar am	-	-	-	-
28 Mar pm	-	-	N	-
05 Apr am	N/S	N	-	-
05 Apr pm	N/SW	S	N	-
12 Apr am	SW	-	-	N
12 Apr pm	SW	-	-	-
21 Apr am	N	N	N	N
21 Apr pm	N	N	N	N
28 Apr am	SW	-	-	-
28 Apr pm	SW	N	-	-
28 May am	S	-	-	-
28 May pm	S	-	-	-

In 1991 aerial surveys were conducted with morning take-offs (10:30) flying south to Coral Bay, returning in the afternoons (14:00 take-off). The current direction was assessed where possible in three sectors, the boundaries being Yardie Creek, Point Cloates and Coral Bay.

1992

Date	Wind Direction	Current direction (2 sectors)	
01-Mar	SW	N	N
14-Mar	SW	N	N
21-Mar	S	S	-
29-Mar	N	-	.
04-Apr	SW	N	N
08-Apr	SW	N	N
14-Apr	S	N	-
21-Apr	-/S	N	N
01-May	S	S	S
09-May	-	-	-
16-May	E	-	S
26-Jun	-	S	S
03-Aug	S	N	-

In 1992 survey flights were flown from the northern end of the reef south to Point Cloates at Ningaloo, with a 10:30 takeoff; the current was assessed in northern and southern sectors, to the north and south of Yardie Creek Gorge.

Results

Winds

The wind records from Cape Cuvier demonstrate the seasonal weather pattern experienced at Ningaloo (Fig 3). During much of the year, prevailing south-easterly trade winds during the night and morning are replaced by stronger south-westerly sea-breezes in the afternoon. The mean wind speed in summer is 7 to 9 m s^{-1}, but this falls to only about 3 m s^{-1} in winter due to the more variable wind directions in that season. Peak wind speeds exceed 14 m s^{-1} in all months. This pattern is essentially similar to that found by Hearn *et al.* (1986) at Carnarvon (25° S) and Learmonth (on the east coast of Exmouth peninsula), allowing for local effects at those two sites.

A strong and persistent southerly wind blows between about September and March, and by April the prevailing winds swing more to the east (particularly during the mornings), delaying the onset of the south-westerly sea-breeze and often giving a period of calm conditions in the middle of the day. In some years, large continental high pressure systems produce strong daytime north-easterly winds in May and June.

Coral spawning

The dates of coral spawning at Ningaloo between 1984 and 1996 are listed in Table 1. Observations collected from divers at different locations have suggested spawning is not necessarily uniform along the reef. In some years, northern reefs of Exmouth Gulf and at Tantabiddi tend to spawn more heavily early in March, whereas the southern reefs (Coral Bay) had heavy spawning in April. In 1992, for instance, there was heavy spawning in Exmouth Gulf on 26-27 March, and very little activity reported from Coral Bay. The second spawning on 24-25 April was very heavy in Coral Bay with formation of extensive slicks. This is the latest date of a heavy spawning yet observed by the authors.

Surface and aerial observations of currents

Preliminary direct observations of currents from boats between 1987 and 1989 suggested that the reef-front current is usually northward during March and early April, and only turns persistently southward during the second half of April. In 1987 for instance, the reef corals spawned on 21-22 March; on 28 March and 4 April there was clear evidence of a northward current, and it was not until 8 April that a southward current was first evident along the reef front.

Aerial surveys conducted from 1990 to 1992 confirmed the presence of the northward current, and also showed that March to April is a transition period from the summer to winter pattern. In 1990 (Table 2), no northward currents were seen after 2 April. In 1991 and 1992, a northward current predominated in March and April, still being evident on 28 April 1991 and 21 April 1992, well after the dates of coral spawning that year. The direction of the current was generally, but not always, the same as the wind on the reef front (*e.g.* southerly wind generating a northward current).

When the northward current was present along the reef front, it was often clear that the Leeuwin Current was strongly pushing southward some 2 km offshore. From the air, a definite line was evident on the water with comparatively calm water near the coast and rougher seas beyond as the southward current pushed against the northward winds (the "wind-versus-current" phenomenon). On calmer days, fingers of clear blue offshore water could be seen meeting the greener turbid water of the reef-front.

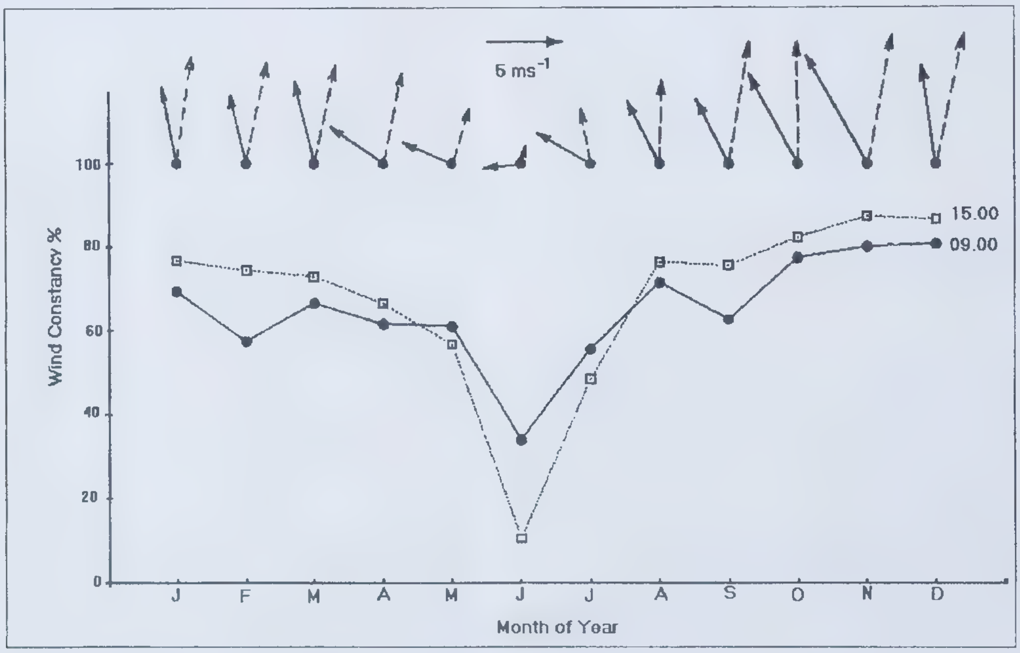

Figure 3. Monthly mean wind vectors at Cape Cuvier (24° 13' S, 113° 23' E) at 09.00 (solid arrows) and 15:00 (dashed), and wind "constancy" (a measure of the persistence of the wind direction) at 09.00 and 15.00 for 1972-75. Data are from the Bureau of Meteorology (Perth, Western Australia).

Satellite imagery of currents

The satellite images presented here are from 1991 and can be related to the data presented from the aerial surveys and the PTT current drogue (see below). Similar patterns have been observed in the subsequent years, 1992 to 1996.

The Leeuwin Current originates north of Exmouth, the satellite imagery often suggesting a "funnelling" of warm water from the north-west, north and north-east down towards the Exmouth region. On occasion, there is a south-westward flow along the Northwest Shelf (as described by Holloway & Nye 1985), but many images also indicate a near-zonal front at the latitude of Northwest Cape, indicating a strong eastward flow towards the Ningaloo Reef, the Eastern Gyral Current described by Wijffels (CSIRO Marine Research, Hobart, personal communication). These sources merge and deflect southwards as the Leeuwin Current, but with considerable spatial and temporal variability. The Leeuwin Current generally therefore becomes identifiable as a boundary current in the Exmouth/Ningaloo area, but is not always well-defined along this section of the coast, particularly during the summer months. As shown by Smith *et al.* (1991), the southward transport of the Leeuwin Current increases south of Shark Bay, and temperatures derived from satellite imagery indicate that the surface thermal contrast between the Leeuwin Current and the cooler offshore water also increases with latitude southwards.

The warm Leeuwin Current and the cool counter-current are visible in many summer/autumn images, particularly south of Point Cloates where the shelf is wide, although further north the inshore current is very narrow and sometimes at the limit of resolution. Further, surface temperature gradients across the Leeuwin Current are weaker during summer than in winter when the current is flowing strongly, so the flow is not always clearly defined in summer images. Nevertheless, the NOAA/AVHRR satellite images depict sea-surface temperatures from which the larger-scale features of the ocean circulation off the Ningaloo Reef can generally be deduced.

As off the south-west coast (Pearce & Pattiaratchi 1999), when the southerly wind stress is very strong during the summer months, the Leeuwin Current weakens and becomes less clearly defined. It tends to move further offshore and a coastal current of cooler water flows northwards from (at least) the southern end of the Ningaloo Tract towards Point Cloates and continues along the reef front. It may be narrow and restricted to the inner shelf (Fig 4A) or can extend well across the shelf and upper slope (Fig 4B,C). Many images show the counter-current continuing eastwards past North-West Cape and the Muiron Islands. In contrast,

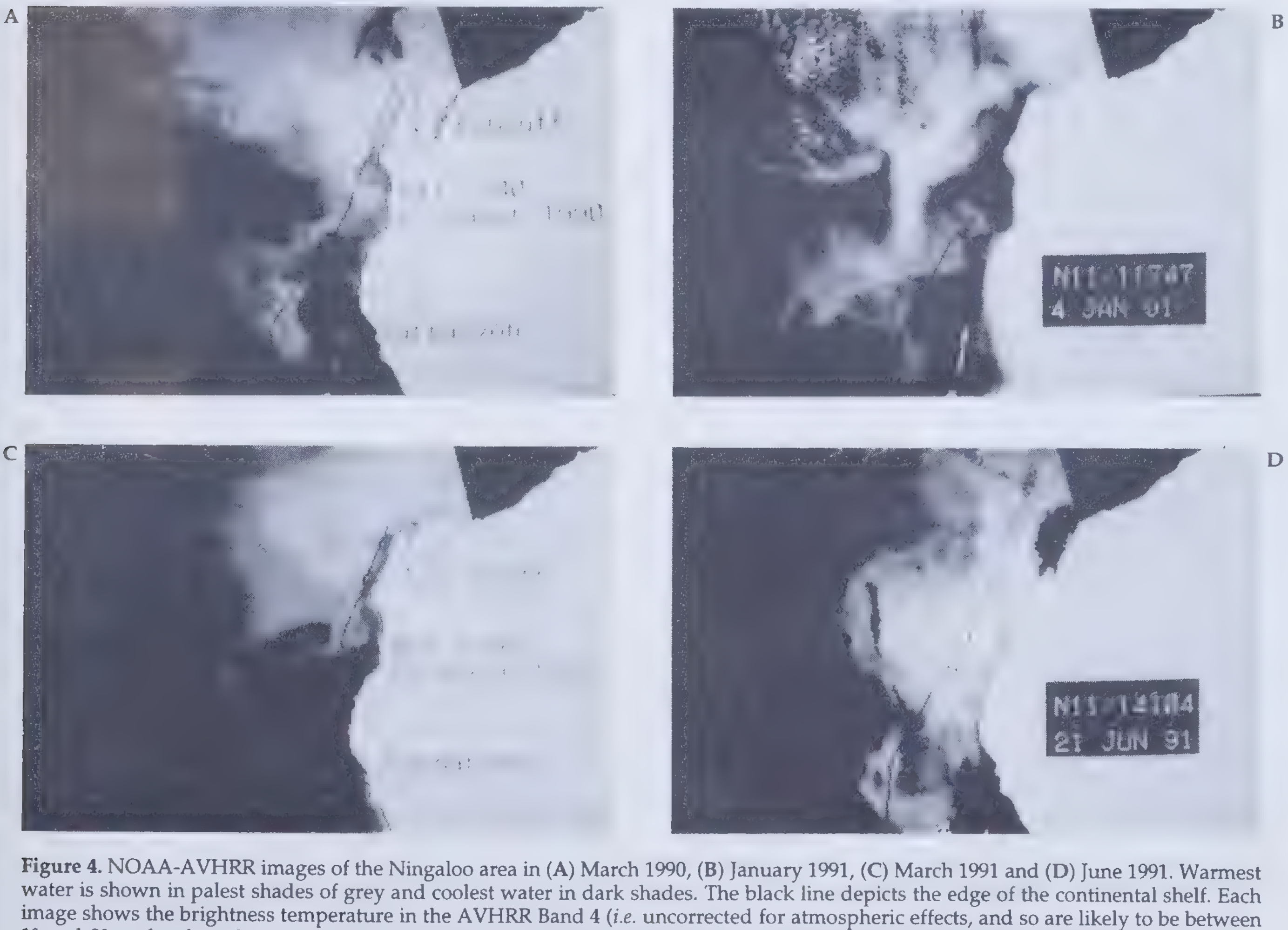

Figure 4. NOAA-AVHRR images of the Ningaloo area in (A) March 1990, (B) January 1991, (C) March 1991 and (D) June 1991. Warmest water is shown in palest shades of grey and coolest water in dark shades. The black line depicts the edge of the continental shelf. Each image shows the brightness temperature in the AVHRR Band 4 (*i.e.* uncorrected for atmospheric effects, and so are likely to be between 1° and 3° cooler than the true surface temperatures). Each image has been enhanced to show specific current details, so there is no particular connection between the temperature/colour scales between the images.

during the winter months when the net southerly winds are relatively weak (Fig 3), the Leeuwin Current flows southward along the continental shelf, spreading across the shelf to the coast and also floods into the bight south of Ningaloo Station (Fig 4D).

A feature of many summer images is an anti-clockwise eddy peeling from the Leeuwin Current and penetrating across the shelf towards the coast in the bight south of Point Cloates and presumably joining the counter-current (Fig 4A,B,C). The significance of this (topographically-induced?) eddy is that it represents a possible mechanism for any biota such as zooplankton or coral spawn which may mix across the shelf into the Leeuwin Current from the northern Ningaloo Reef to re-circulate back into the coastal system via the northward countercurrent.

Sea-surface temperatures on the open continental shelf off Ningaloo range from about 27° C between February and April to 22° C in August/September (Marine Climatic Atlas of the World, CD-ROM, US Naval Oceanography Command, Ashville, NC). Boat measurements of water temperature were available in March 1991 confirming the impression from aerial and satellite data. The turbid "green" water on the reef front was repeatedly measured at 26.3 °C to 26.5 °C with a sharp rise in temperature to 27.1 °C on crossing into the clear oceanic water offshore.

Current drogue trajectory

On 11 April 1991, four days after a coral spawning event, the ARGOS satellite PTT, which detached from a whale shark close to the northern end of the reef, was taken south for most of the period it was tracked in the Leeuwin Current, against the strong southerly winds normally prevailing at that time of year (Fig 3), indicating that the "windage" was relatively small. However, it was initially carried north and circled in an eddy off North-West Cape for nearly two days before being taken rapidly south (at up to 45 cm s^{-1}, or almost a knot) in the Leeuwin Current (Fig 5). On 18-19 April it was brought closer inshore by an anti-clockwise eddy or current meander off Coral Bay and then travelled north for two days before being taken south again towards Cape Cuvier. This trajectory showed the reef front current flowing northwards (off North-West Cape and off Coral Bay) and the Leeuwin current flowing strongly southwards offshore, as well as indicating some degree of cross-shelf exchange/recirculation of water. A satellite image for 4 April that year clearly shows an anti-clockwise eddy near Coral Bay and the counter-current running northwards along the Ningaloo reef (Fig 6).

Current meters

Near-bottom currents at the shelf-break were measured by CSIRO during the Leeuwin Current Interdisciplinary Experiment (LUCIE) between September 1986 and August 1987. The current meter was 15 m above the seabed in 118 m water depth (Boland *et al.* 1988). Although the mooring may not have been in the strongest part of the Current, the flow was southward at between 10 and 40 cm s^{-1} for almost the entire year, with strongest currents (up to 60 cm s^{-1}) in May and June.

Measurements from a current meter further down the continental slope between 1994 and 1996 also indicated a predominantly southward flow (strongest from February to April) with sporadic reversals between August and October when the Leeuwin Current had weakened (D R Tippins & M Tomczak, Flinders Institute of Atmospheric and Marine Sciences, personal communication). Peak near-surface current speeds were of order 1 m sec^{-1}, and below about 150 m depth there was a northwards counter-current as found earlier by Thompson (1984).

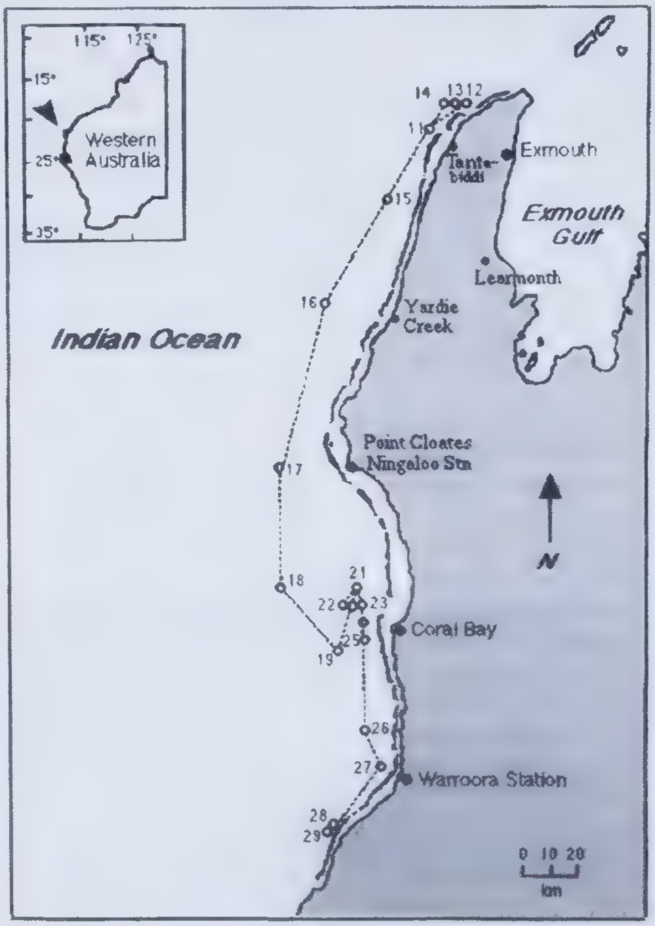

Figure 5. The trajectory of a satellite PTT transmitter which had become detached from a whale shark in April 1991, effectively acting as a current drogue. The date of each daily position (the first fix of the day, usually 0600 to 0700 GMT) is shown next to each point.

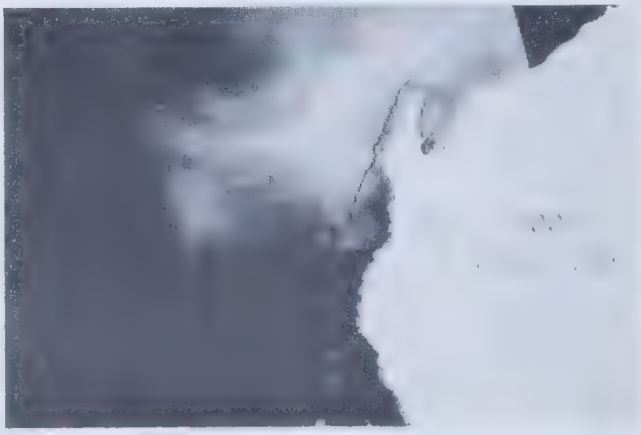

Figure 6. NOAA-AVHRR image of the Ningaloo area in April 1991 clearly showing the counter-clockwise eddy south of Coral Bay, and the northward current on the wide shelf south of Point Cloates. Other details as in Fig 4.

Discussion

The preliminary observations made in autumn each year at Ningaloo showed that a northward cool coastal current flowed during March and early April, the period of the annual mass spawning of corals. The observations made on the water and from aircraft were confirmed by studying the satellite imagery from the same period. More extensive studies of the satellite imagery then showed that the northward flowing current is predominent for the majority of the year (8 months). It should be appreciated that the images presented in this paper are a small sample of the many images studied.

The northward counter-current predominates on the reef-front from September through the summer till mid-April, and is thought to be largely driven by the South-East (Trade) winds and the strong diurnal coastal south-westerly sea-breezes (Fig 3). We propose that this current should be called the "Ningaloo Current". In the southern reef where the continental shelf is wide, the current is broad based, up to 30 km wide, and more easily seen on satellite imagery. To the north of Point Cloates where the seabed shelves more rapidly, the northward current is often less than 2 km in width, and at times too narrow for resolution by satellite imagery.

The cold water temperature anomalies observed by Simpson & Masini (1986) have given rise to speculation regarding upwelling at Ningaloo. There has been no convincing evidence of upwelling from the satellite imagery. However, the counter-current model gives a possible explanation of how the anomalies might occur. The Ningaloo Current is a cool current and the temperature of water travelling north will depend on the degree of mixing with the warmer Leeuwin Current offshore, and the amount of recirculation caused by eddies such as the one observed off Coral Bay. Indeed, this eddy demonstrates how upwelled water masses from offshore might be advected to the reef front. Hearn *et al.* (1986) were concerned that large temperature gradients would be required to produce such an anomaly. However, in the field, a gradient of 0.5 °C in a few metres has been measured between different water masses off Tantabiddi.

The initial observations were made in autumn at the time of transition from the summer to winter pattern. The timing of this transition varies from year to year depending on weather conditions, and may be critical to biological processes in the region. The northward alongshore flow acts as a counter-current to the Leeuwin Current, and sometimes extends eastwards past North-West Cape. These opposing currents generate a re-circulation of water in the region. To the north of the Cape there are strong tidal influences produced by the ebb and flow of tides in Exmouth Gulf. Further south the prominence of Point Cloates is conducive to the formation of a topographic eddy in the Leeuwin Current which has been observed on many satellite images, bringing warm water into the southern end of the Ningaloo Reef tract.

The presence of the Ningaloo Current and this circulatory movement of water has major implications for various biological systems in the region. Scientists have long argued about the enigma represented by the high productivity of coral reefs existing in waters that are low in essential nutrients such as phosphate and nitrogen (Hatcher 1988; Kinsey 1991). The production of spawn by the coral is a major annual event of lipid and protein production, so the mass spawning of a coral reef represents a significant export of protein, and therefore nitrogen, from the reef itself.

Theories regarding coral spawn dispersal at Ningaloo have hitherto assumed that the spawn from the Ningaloo Reef is carried south by the strong Leeuwin Current (Simpson 1985, 1991) as a unidirectional flow of genetic material. Our observations in the field over the period of this study have shown that the reef front current is in fact northward during at least the March spawning and usually during the April spawning as well, especially if this occurs early in the month. The track of the PTT current drogue demonstrates the situation in 1991. It was deployed on 11 April, after the coral had spawned on 7-8 April, and clearly demonstates a likely pattern for the dispersal of coral spawn that year. The drogue was eventually brought inshore towards the reef and travelled northward off Coral Bay. We suggest that the nearshore counter-current system observed at Ningaloo during the period of the annual mass spawning is responsible for maintaining a large proportion of the exported protein within the Ningaloo Reef system and may therefore be important for the survival of the reef itself.

Many other marine organisms apart from the coral spawn at this time of year. One example is the mass epitokous spawning of polychaete worms which occurs synchronously with the corals. It has been proposed that this mass spawning releases large amounts of protein into the waters of the region, boosting the zooplankton food

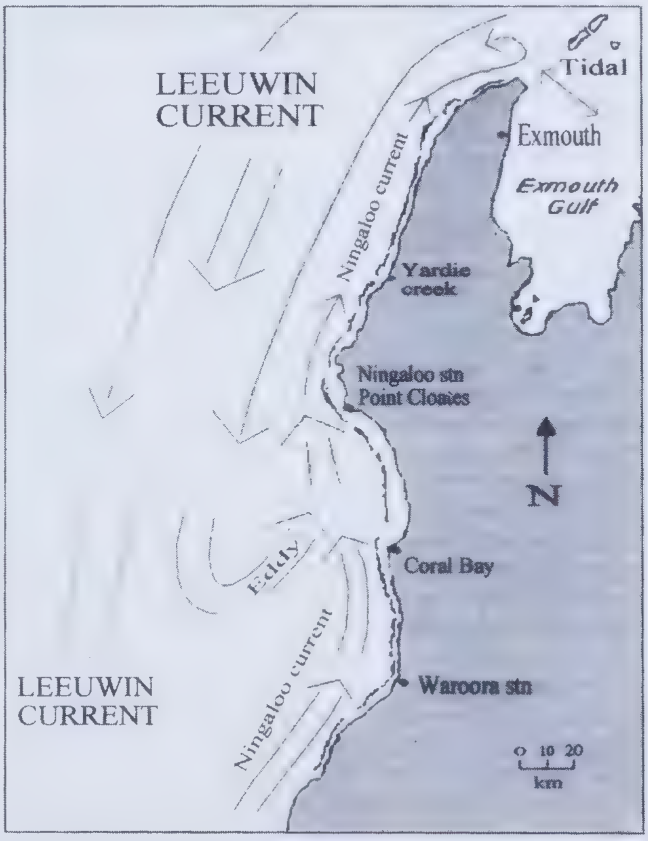

Figure 7. Proposed current mechanisms at Ningaloo Reef operating principally from September until mid-April.

chain at this time of year (Taylor 1989, 1996). There are likely to be inter-annual variations in the strength and transport of the counter-current, largely resulting from variability in the winds and in the strength and position of the Leeuwin Current, and the productivity of the area may accordingly be affected. The abundance of filter-feeding marine animals such as the whale shark (*Rhincodon typus*) may reflect the abundance of zooplankton in the area. Indeed, the presence of whale sharks could be looked upon as an indicator of zooplankton abundance.

The first observations of a whale shark surface-feeding during the day at Ningaloo were made in March 1991, 14 days after the March coral spawning. A strong northerly current was sweeping huge swarms of spawning krill *Pseudeuphausia latifrons* along the reef-front. The whale shark charged through the swarms of krill with its mouth agape, trapping its prey against the water surface; this surface feeding behaviour is more common at dusk (Taylor 1994).

Studies of whale sharks at Ningaloo are incomplete, having concentrated mainly on the northern reef, north of Point Cloates (Taylor 1989, 1994, 1996). The area was studied in greater detail with aerial surveys from 1990 to 1992. The surveys showed that while the sharks may be spread all along the reef in the early part of the season, they would aggregate into one area, during April. This aggregation is usually along the northern reef, close to Tantabiddi, but in 1989 it was further south off Yardie Creek, and in 1990 no aggregation was found at all in the northern reef area (Taylor 1996). These data suggest some correlation between the presence of the northerly counter-current and the abundance of whale sharks at the northern end of the reef. April 1990 was a season of very low whale shark sightings; the reef front current during April was predominantly southwards (Table 2). During the following two years, 1991 and 1992, when the aerial surveys showed good evidence of the northerly counter-current throughout April, large numbers of whale sharks were encountered (Taylor 1996). More recently, 1995 was a relatively poor whale shark season with low numbers of encounters reported by commercial operators; it was also a year of unseasonal calm, humid weather and direct observation showed no evidence of a northward current on the reef front in early April, with a strong southward current noted by the 8-9 April.

The 1998 whale shark season had very low numbers in the northern reef area, similar to 1990. A coastal trough formed in March and persisted into April, bringing calm sea conditions and early rain. The south-westerly sea-breeze was weak or absent throughout that period, and satellite images show little evidence of either Leeuwin or Ningaloo Currents. Sea temperatures on the reef front were greater than 29 °C, which is 2 °C hotter than any previous year and consistent with the absence of the cool Ningaloo current.

Our observations show that the northward counter-current is well established during the summer months with the strong southerly winds. April is a month of transition to the winter pattern, and in early winter, when north-easterly winds are common, the southward Leeuwin current predominates. In June 1993, much publicity was given to the "fish feeding frenzy" at Cape Cuvier, to the south of the Ningaloo Tract, where sharks and Bryde's whales were seen feeding on huge schools of anchovies. It may be relevant that on 19 May that year, a massive school of anchovies estimated at one kilometre in diameter was reported by charter boats and aircraft off the northern Ningaloo Reef at Tantabiddi (Fig 1). The school was surrounded by sharks, manta rays and whale sharks. It is possible that this was the same fish school, taken south by the Leeuwin current, as the one seen the following month beneath the cliffs at Cape Cuvier. Based on the current drogue observations it would take 10 days (at a speed of 20 cm s^{-1}) for such a fish school to be taken south to Cape Cuvier. It can be seen that the high productivity of the Ningaloo tract in the autumn is eventually dispersed southwards by the Leeuwin current during the winter months, and may affect the productivity of the whole west coast. A second satellite PTT was deployed in March 1991 but malfunctioned; it was recovered from a beach at Lancelin (100 km north of Perth) only 4 months later, representing a southwards transport of order 10 cm s^{-1}, which compares well with current estimates by Hutchins & Pearce (1991).

Comparing the Ningaloo and Barrier Reefs, Simpson (1991) proposed that the natural selection of corals that spawn at this time of year on the west coast of Australia reflects historical breeding patterns, and are a result of ocean currents emanating from the Indonesian Archipelago. The strong Leeuwin Current brings autumn spawners down the west coast, while spring spawners are taken eastwards to the Great Barrier Reef. Extrapolating from this theory, natural selection may also operate at a more local level. Organisms that spawn when the Leeuwin Current flows strongly on the reef front would have their progeny moved progressively southwards, and could only survive on the reef through replacement from further north (Simpson 1991). During the period that the counter-current operates, however, spawn may be maintained within the reef system allowing local settlement to occur. Organisms, and in particular corals, that spawn when the counter-current is operating would be more likely to survive on the reef. Hence, it is possible that the counter-current system through natural selection may influence the timing of the reef spawning.

We suggest that there are 3 current zones across the continental shelf off Ningaloo (Fig 7); the warm southward Leeuwin Current, flowing along the outer shelf/upper slope and driven by an alongshore pressure gradient (Godfrey & Ridgway 1985); a seasonal wind-driven northward inner-shelf counter-current, the Ningaloo Current (this study); and a wave/wind/tidally-driven flow within the nearshore reef system (Hearn *et al.* 1986). With the present interest in the Cape Range Peninsula of the oil industry, the area could in the future see the establishment of off-shore oil tanker terminals. It is therefore of vital importance that a full understanding of current mechanisms at Ningaloo is developed to assist the industry in oil spill contingency planning.

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Seven new species in *Acacia* section *Lycopodiifolia* (Mimosaceae)

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Abstract

In preparation for a treatment of *Acacia* sect *Lycopodiifolia* for the 'Flora of Australia', seven new species are described and illustrated; *Acacia anasilla, A. capillaris, A. hypermeces, A. mitodes, A. repens, A. smeringa* and *A. zatrichota.* All occur in the Kimberley, Western Australia, with *A. repens* extending to the Northern Territory. A key to all species of *Acacia* with whorled phyllodes is provided.

Introduction

Acacia section *Lycopodiifolia* was described by Pedley (1978) to accommodate a group of tropical and subtropical Australian wattles with whorled phyllodes, prominent stipules and flowers in solitary heads. In an earlier paper (Pedley 1972), he recognised 12 species, but two of these, the non-tropical *A. baueri* Benth and *A. cedroides* Benth, are now considered better placed in section *Phyllodineae* (Maslin & Stirton, 1998; B R Maslin, Western Australian Herbarium, personal communication). Forster (1990) described the new species *A. porcata* from Queensland. In the course of preparing an account of section *Lycopodiifolia* for the 'Flora of Australia', seven new species were recognised and I describe them here. All occur in the Kimberley, Western Australia, and *A. repens* is also recorded for the Northern Territory. On the basis of collections made so far, all of these seven species are considered rare. The coding used here for conservation status of these seven species follows Briggs & Leigh (1996). Under the Conservation Codes for Western Australian Flora of the Department of Conservation and Land Management, all of these seven species are Priority Two. The sectional name is spelt *Lycopodiifolia* in accordance with Article 22.5 of the 'International Code of Botanical Nomenclature' (Greuter *et al.*, 1994).

This study was based on a study of the morphology of habit, vegetative parts, flowers and fruits of all taxa in the section, from most Australian herbaria as well as the Royal Botanic Gardens, Kew. A key to all species of *Acacia* with whorled phyllodes is provided.

Systematics

Acacia sect **Lycopodiifolia** Pedley, *Austrobaileya* 1:82 (1978) (as *Lycopodiifoliae*)

Racosperma sect *Lycopodiifolia* (Pedley) Pedley, *Bot J Linn Soc* 92:240 (1986). Type: *A. lycopodiifolia* Cunn ex Hook.

Phyllodes in whorls of 6–27, less than 2 cm long, terete or slightly flattened, commonly abruptly mucronate but not pungent, without prominent nerves; stipules usually prominent, the base commonly persistent after phyllode falls. Flowers 5-merous, in solitary axillary heads; 6–50 flowers per head. Calyx shortly or moderately lobed. Pod flat with ± prominent margins. Seed arillate.

A section of 18 species, mainly of tropical and subtropical Australia including semi-arid and arid regions, readily recognised by the small, whorled phyllodes with prominent stipules. Seedlings have the characteristic alternate, bipinnate leaves which change abruptly to whorled phyllodes. In most species the mucro of the phyllode wears off after a year or so. Several taxa are highly variable and probably further taxa should be recognised. The section should be thoroughly revised, with extensive field work.

Descriptions of the species

Acacia anasilla A S George, sp nov (Fig 1 A–C)

Inter species alias sectionis *Lycopodiifoliae* habitu elatiore (frutex ad 2 m altus), indumento densissimo hispido, et capitulis grandibus (floribus 40–50), praecipue differt. Stipuli recti, 1.5–2 mm longi. Lobi calycis subulati, glabri. Lobi corollae striati, hispidi.

Typus: Winnama Spring, Mabel Downs Station, WA, 17° 11' S, 128° 15' E, 15 November 1989, *K A Menkhorst 835*; holo: PERTH 01187465; iso: CANB, DNA, MEL1582581.

Erect *shrub* to 2 m. *Stems* densely white-hispid; internodes 2–10 mm long, on main stems to 16 mm. *Phyllodes* 15–20 per whorl, spreading to gently recurved or the lower erect, somewhat flattened when dried with a midrib evident on abaxial surface, ± straight, slender, 5–10 mm long, hispid; mucro 2–4 mm long, ± incurved, commonly with viscid droplets; stipules erect, subulate, 1.5–2 mm long. *Peduncles* 1.5–3 cm long, hispid. *Heads* 40–50-flowered; bracteoles subulate, 2.5–3 mm long, glabrous. *Calyx* ca. 0.8 mm long, glabrous; lobes subulate, short. *Corolla* 2–2.3 mm long; lobes ± striate, hispid in upper half. *Pod* sessile or on stipe to 1.5 mm long, 2–3.5 cm long, 5–6 mm wide, glabrous. *Seeds* 3–10 per pod, longitudinal, ca. 4 mm long; aril large; pleurogram closed.

Key to taxa of *Acacia* with regularly whorled phyllodes

(includes four taxa not belonging to section *Lycopodiifolia*, marked *)

1 Phyllodes pungent (south-western WA)

2 Flowers 5-merous

3 Stems ribbed; phyllodes 10–30 (–40) mm long; heads cream to pale yellow; pods striate, 2.5–3.5 mm wide ...... **_A. cedroides_***

3 Stems ribless; phyllodes normally 8–19 mm long, sometimes shorter; heads golden; pods not striate, 5–7 mm wide ...... **_A. sphacelata_ subsp _verticillata_***

2 Flowers 4-merous; stems ribless; phyllodes 8–12 (–15) mm long; heads pale yellow; pods not striate, 3–4 mm wide ...... **_A. simulans_***

1 Phyllodes not pungent, though commonly abruptly mucronate (northern arid & tropical Australia, NSW)

4 Plant prostrate

5 Flowers 6–8 per head; calyx 1.8–2 mm long ...... **_A. mitodes_**

5 Flowers 16–25 per head; calyx 0.5–0.8 mm long

6 Phyllodes 6–9 per whorl, prominently uncinate; stipules 1.5–2 mm long; calyx lobes triangular ...... **_A. repens_**

6 Phyllodes 9–12 per whorl with straight or slightly curved mucro; stipules ca. 1 mm long; calyx with irregular, rounded lobes ...... **_A. hypermeces_**

4 Plant erect or spreading, occasionally procumbent

7 Petals not or obscurely striate

8 Stipules typically absent, if present then minute; phyllodes commonly 5–7 per whorl ...... **_A. baueri_***

8 Stipules prominent, 0.5–4.5 mm long, setaceous; phyllodes commonly 8 or more per whorl

9 Calyx glabrous

10 Plant viscid; phyllodes 6–12 per whorl; stipules 0.8–1.5 mm long; flowers 25–40 per head ...... **_A. spondylophylla_**

10 Plant not viscid; phyllodes 14–20 per whorl; stipules 3–4.5 mm long; flowers 20–25 per head ...... **_A. capillaris_**

9 Calyx lobes hairy at least in part

11 Calyx less than 1 mm long

12 Phyllodes 12–15 per whorl; calyx 0.4–0.6 mm long; stem indumentum of yellow hairs; seeds transverse ...... **_A. hippuroides_**

12 Phyllodes 16–20 per whorl; calyx 0.7–0.8 mm long; stem indumentum of white hairs; seeds longitudinal ...... **_A. zatrichota_**

11 Calyx more than 1 mm long

13 Calyx 1.2–1.5 mm long

14 Phyllodes in whorls of 10–15, 2–7 mm long; mucro 2.5–3 mm long; calyx lobes obtuse ...... **_A. smeringa_**

14 Phyllodes in whorls of 15–20, 8–15 mm long; mucro ca. 1–1.5 mm long; calyx lobes acute or acuminate ...... **_A. longipedunculata_**

13 Calyx 1.7–2.2 mm long ...... **_A. porcata_**

7 Petals striate

15 Calyx lobes broadly triangular or rounded

16 Flowers 10–25 per head; seeds longitudinal

17 Phyllodes 14–18 per whorl; stipules 3–4.5 mm long; pod not viscid ...... **_A. capillaris_**

17 Phyllodes 8–11 per whorl; stipules 0.4–3 mm long; pod viscid

18 Flowers 20–25 per head; stems velvety-tomentose ...... **_A. chippendalei_**

18 Flowers usually 10–20 per head; stems puberulous, pubescent or glabrous ...... **_A. galioides_**

16 Flowers 25–35 per head; seeds transverse ...... **_A. orthotricha_**

15 Calyx lobes linear

19 Phyllode mucro 2–4 mm long; flowers 40–50 per head ...... **_A. anasilla_**

19 Phyllode mucro less than 1.5 mm long; flowers usually fewer than 40 per head

20 Phyllodes usually 2–5 mm long, occasionally to 9 mm; stems not viscid

21 Phylodes 10–14 per whorl; mucro curved, commonly 1–1.5 mm long; seeds longitudinal ...... **_A. lycopodiifolia_**

21 Phyllodes 6–10 per whorl; mucro oblique, to 0.2 mm long, or absent; seeds transverse or slightly oblique ...... **_A. adoxa_**

20 Phyllodes usually 8–15 mm long, occasionally as short as 6 mm; stems, or at least stipules, viscid

22 Stipules 2–3 mm long; phyllodes flattened, or channelled above; calyx 0.9–1.5 mm long ...... **_A. perryi_**

22 Stipules <2 mm long; phyllodes terete; calyx 0.6–0.9 mm long ...... **_A. asperulacea_**

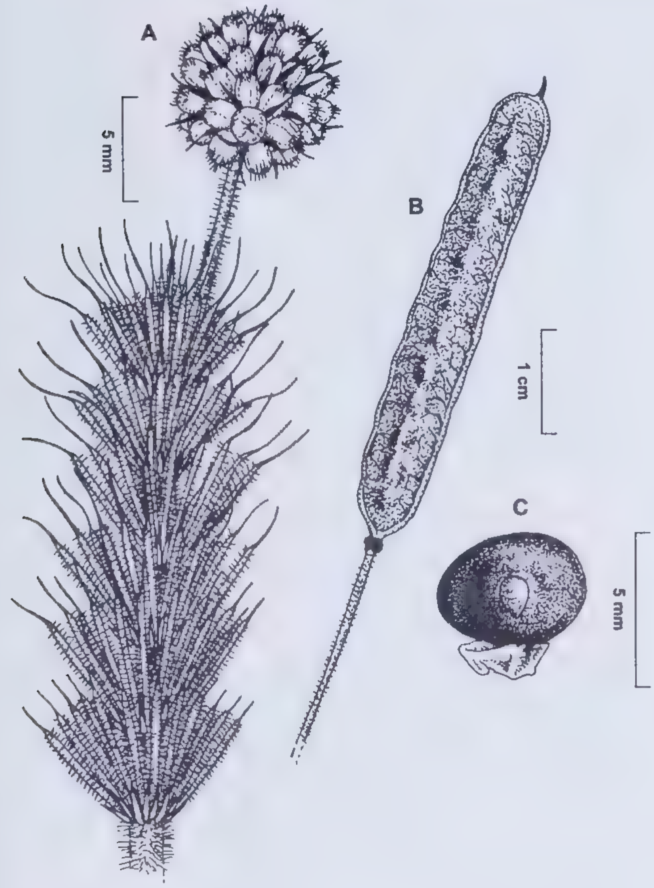

Figure 1. **A–C**, *Acacia anasilla*. **A**, portion of flowering branchlet; **B**, pod; **C**, seed.

Distribution and habitat Recorded from Mabel Downs and Springvale Stations and Dimond Gorge on the Fitzroy River, WA (Fig 2). Grows on sandstone hillsides in *Eucalyptus brevifolia* woodland. Flowers in Oct.–Nov.

Conservation status 2R-

Etymology Specific name from the Greek *anasillos* (a bristling hair), in reference to the overall appearance of the plant.

Other collections examined Dimond Gorge, ca. 70 km NE of Fitzroy Crossing, Fitzroy River, *A C Beauglehole 53813* (BRI, PERTH); NW of Springvale Station, *M Lazarides 5068* (CANB, MEL); Ord River, 1888, - *Nyntasy* (MEL); Halls Creek, 1895, *W D Mansbridge* (MEL).

Affinities This species has more flowers per head than others of the section. It resembles *A. lycopodiifolia* but is larger in all its vegetative parts. It is also similar to *A. smeringa*, differing especially in its striate corolla and narrow calyx lobes. The early collections from Ord River and Halls Creek possibly have general locality data.

Acacia capillaris A S George, sp nov (Fig 3 A-C)

Ad *Acaciam lycopodiifoliam* Cunn ex Hook affinis, a qua stipulis longioribus (3–4.5 mm longis) setaceis; phyllodiis in quoque verticillo 14–18; pedunculis longioribus (14–17 mm longis); calyce obscure striato lobis triangularibus; et legumine breviter stipitato, praecipue differt.

Typus: W of Mt Bell, [King] Leopold Range, WA, 17° 09' S, 125° 17' E, 5 May 1988, *R J Cranfield* 6719 (holo: PERTH 00909661; iso: CANB, K).

Erect *shrub* 40 cm tall. *Stems* pilose with spreading white hairs to 1 mm long; internodes 8–12 mm long, shorter on some branchlets. *Phyllodes* 14–18 per whorl, erect, somewhat flattened adaxially, 5–6 mm long, with an oblique to almost uncinate mucro 0.3–0.5 mm long, pilose with ascending to spreading white hairs; stipules setaceous, 3–4.5 mm long, spreading, yellowish. *Peduncles* 14–17 mm long, pilose with spreading white hairs that are more flexuose than on vegetative parts. *Heads* 15–20-flowered; bracteoles subulate, 2–2.5 mm long, glabrous. *Calyx* 0.8-1 mm long, divided for ca. half length into

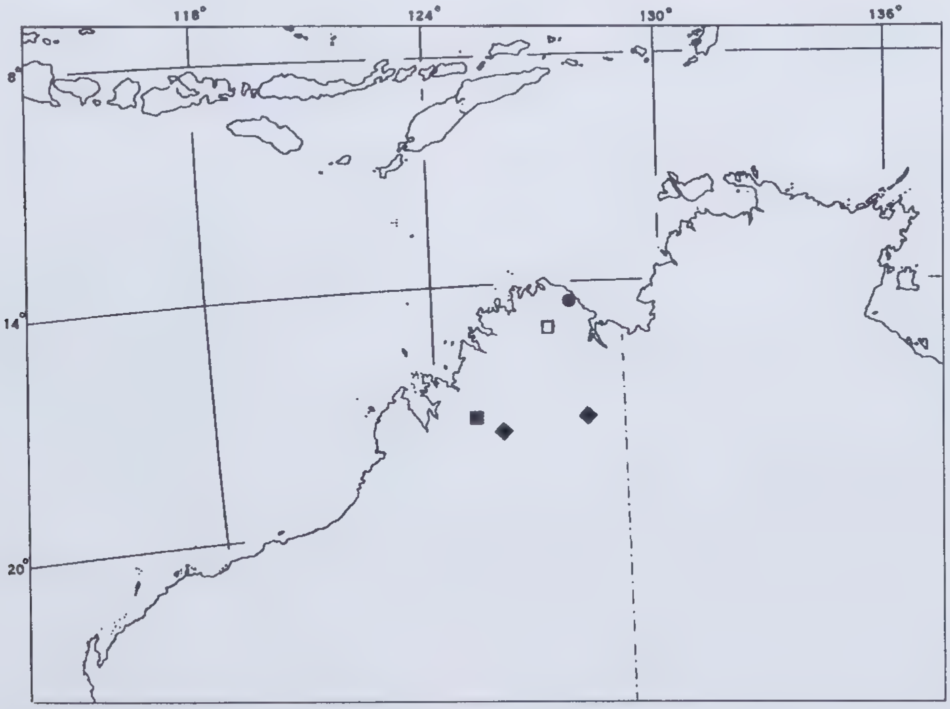

Figure 2. Distribution of *Acacia anasilla* (◆), *A. capillaris* (■), *A. hypermeces* (●) and *A. mitodes* (□).

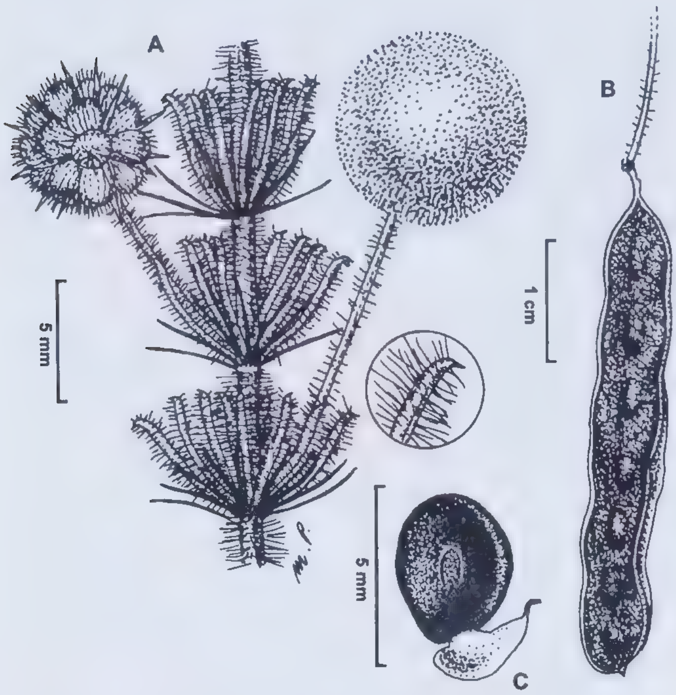

Figure 3. A–C, *Acacia capillaris*. **A**, portion of flowering branchlet with apex of phyllode (insert); **B**, pod; **C**, seed.

triangular obtuse lobes, not or obscurely striate, glabrous. *Corolla* 2–2.4 mm long, the lobes striate, pilose. *Pod* on stipe 2–3 mm long, linear, flat but raised over seeds, not viscid, 1.5–4 cm long, 4–4.5 mm wide, glabrous, brown; margin slightly thickened. *Seeds* 2–8 per pod, longitudinal, obliquely elliptic, 3.5 mm long, black; pleurogram distinct, open, ca. 1 mm long; aril nearly 2 mm long, cupular, offset to one side; funicle very small.

Distributicn and habitat Known from Mt Bell and Scott Gorge in the Kimberley, W.A. (Figure 2). Grows in red-brown clay over granite, under *Livistona* palms near creek, and on rocky slopes among *Triodia*. Flowers in May.

Conservation status 2K-

Etymology Specific epithet taken from the Latin *capillaris* (hair- or thread-like), in reference to the fine stipules.

Other collection examined Scott Gorge, 17° 05' S, 125° 16' E, *M J Sands 4768* (K, PERTH).

Affinities This species is closely related to *A. lycopodiifolia* Cunn ex Hook in its long mucro of the phyllode, striate hairy corolla and pod with longitudinal seeds, but may be distinguished especially by the long, setaceous stipules. It may be distinguished further by the more numerous phyllodes in the whorl, obscurely striate calyx with triangular lobes, and shortly stipitate pod.

Acacia hypermeces A S George, sp nov (Fig 4 A,B)

Ad *Acaciam repentem* A S George affinis, a qua indumento densiore in apice corollae includente; phyllodiis per verticillo pluribus; calyce longiore breviter et irregulariter lobato; et stipite leguminis longiore (ad 4 cm longo), differt.

Typus: mouth of Berkeley River, WA, 14° 21' S, 127° 46' E, 9 Sept 1992, *K F Kenneally 11313* (holo: PERTH 02250594; iso: CANB, K).

Prostrate *shrub* to ca. 1 m wide, the branches, phyllodes and corolla apex openly hispid; internodes 3–10 mm long on upper stems, up to 26 mm on main stems. *Phyllodes* 9–12 per whorl, spreading to ascending, with straight or slightly curved mucro 0.2–0.3 mm long, flat with 1 adaxial and 2 abaxial grooves, commonly 8–15 mm long; stipules subulate, ca. 1 mm long, spreading. *Peduncles* 10–26 mm long, openly hispid. *Heads* commonly 16–21-flowered; bracteoles ovate to lanceolate, acute, 1 mm long, glabrous. *Calyx* 0.8 mm long; lobes very short, rounded-irregular, with midrib. *Corolla* 2 mm long, striate throughout, hispid at apex. *Pod* stipitate, 3–4 cm long, 5–6 mm wide, glabrous; margin slightly thickened. *Seeds* ca. 6 per pod, longitudinal, 3–4 mm long; pleurogram elliptic, closed; aril boat-shaped; funicle small?.

Distribution and habitat Known only from the type and a nearby locality in the Kimberley, WA. (Fig 2), growing in alluvial sand over sandstone rocks. Flowers in June.

Conservation status 2K-

Etymology Specific epithet from the Greek *hypermekes* (very long), in reference to the stipe of the legume.

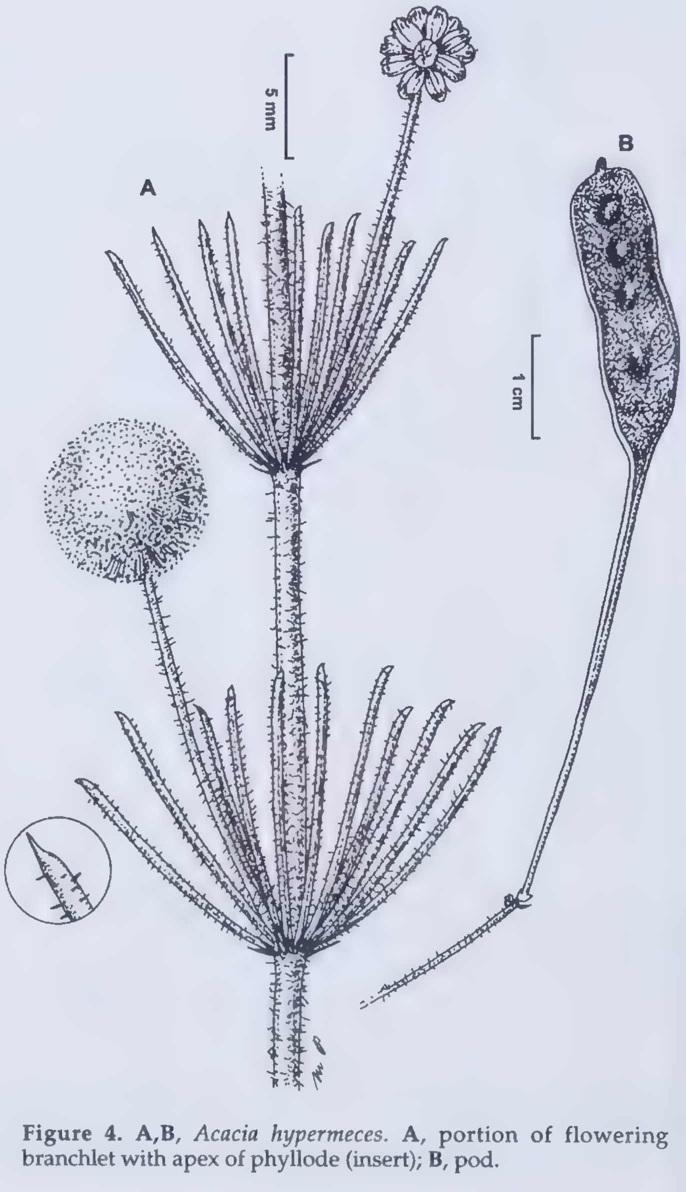

Figure 4. A,B, *Acacia hypermeces*. **A**, portion of flowering branchlet with apex of phyllode (insert); **B**, pod.

Affinities This is related to *A. repens* with which it shares the prostrate habit but from which it is distinguished by the more extensive indumentum including that on the corolla apex, by the greater number of phyllodes per whorl, by the longer, irregularly lobed calyx and by the very long stipe of the legume.

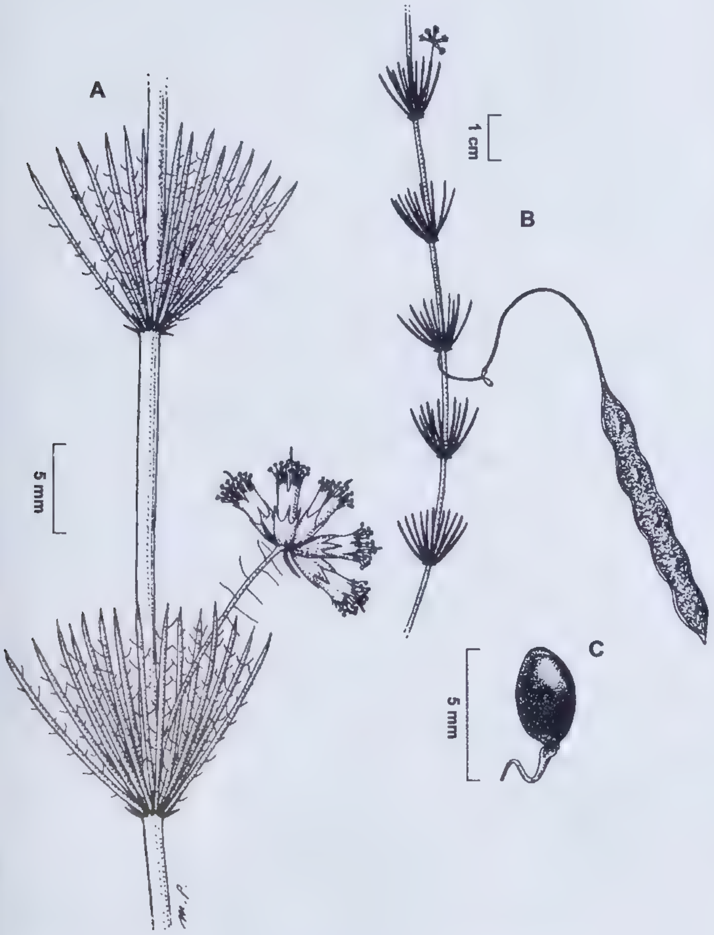

Figure 5. A-C, *A. mitodes.* **A**, portion of flowering branchlet; **B**, pod.; **C**, seed.

Acacia mitodes A S George, sp nov (Fig 5 A-C)

Inter species sectionis *Lycopodiifoliae* habitu prostrato, capitulis paucifloris (floribus 6–8 per capitulum) distinguitur; ad *A. hypermeces* A S George arcte affinis, sed calyce longiore (1.8–2 mm longo) lobis triangularibus, phyllodiis per verticillum numerosioribus (12–17), caulibus glabris, et stipulis longioribus (1.5–1.8 mm longis), praecipue differt.

Typus: Carson Escarpment, Drysdale River National Park, WA, 14° 49' S, 126° 49' E, 2 June 1996, *A A Mitchell 4404* (holo: PERTH 05199956; iso: CANB, K).

Prostrate *shrub*. *Stems* glabrous; internodes 19–30 mm long. *Phyllodes* 12–17 per whorl, erect to gently incurved, terete, acute with mucro ca. 0.2 mm long, 12–19 mm long, sparsely setose; stipules subulate, 1.5–1.8 mm long, erect to somewhat spreading, light brown. *Peduncles* 15–19 mm long, sparsely pilose. *Heads* 6–8-flowered; bracteoles navicular, ca. 1 mm long, glabrous. *Calyx* 1.8–2 mm long, smooth, glabrous; lobes triangular. *Corolla* 2.3–2.5 mm long, smooth, glabrous except setose lobes. *Pod* on stipe 45–55 mm long, 3–5 cm long, 7–8 mm wide, glabrous; margins slightly thickened. *Seed* (immature) longitudinal.

Distribution and habitat Known only from the type locality in the Kimberley, WA (Fig 2). Grows in woodland at top of a sandstone cliff. Flowers in May–June.

Conservation status 1KC-

Etymology The specific name is from the Greek *mitodes* (thread-like), in reference to the long, filiform stipe of the pod.

Affinities Distinguished especially by the few-flowered heads. Closely related to *A. hypermeces*, differing also in the longer calyx, more phyllodes per whorl and longer stipules.

Acacia repens A S George, sp nov (Fig 6 A, B)

Ab speciebus aliis *Acaciae* sectionis *Lycopodiifoliae* habitu prostrato glabro praeter ramos et pedunculos parce hispidos, et corolla prominenter striata, praecipue differt.

Typus: Carr Boyd Range, ENE of Dunham River Station homestead, WA, 16° 14' S, 128° 29' E, 12 March 1978, *M Lazarides 8519* (holo: CANB, iso: BRI, DNA).

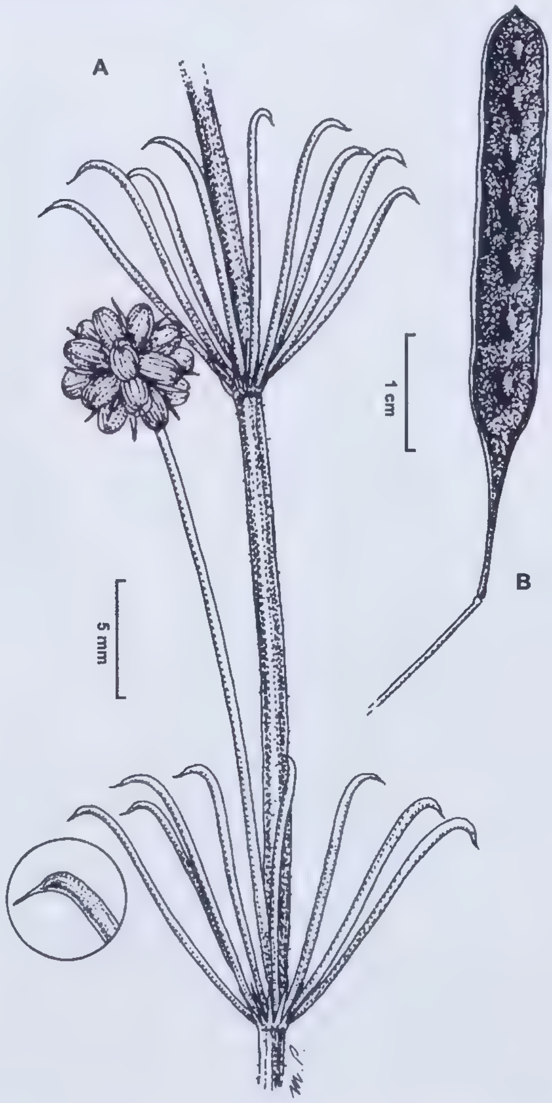

Figure 6. A,B, *Acacia repens.* **A**, portion of flowering branchlet with apex of phyllode (insert); **B**, pod.

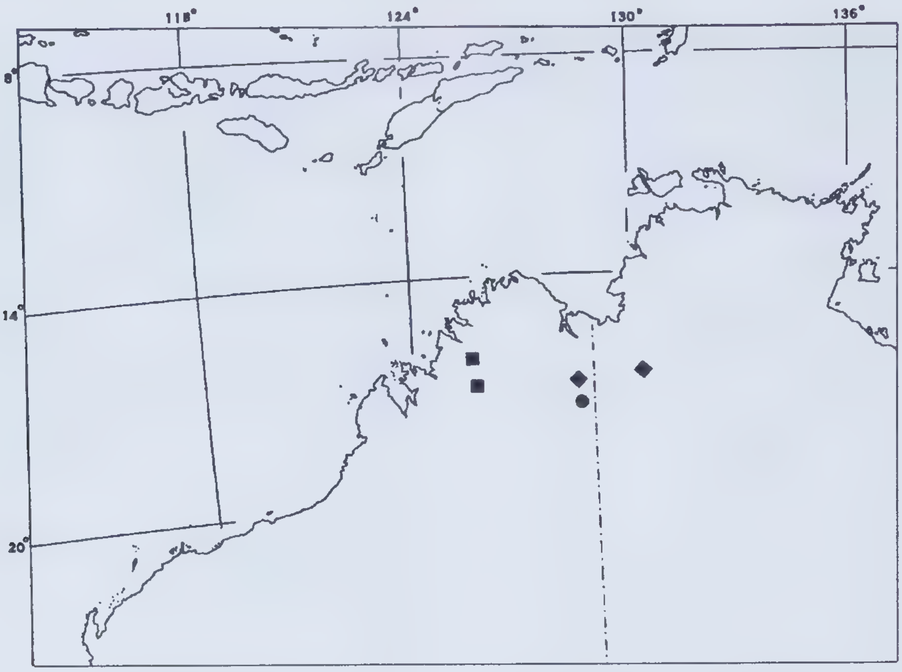

Figure 7. Distribution of *Acacia repens* (◆), *A. smeringa* (■) and *A. zatrichota* (●).

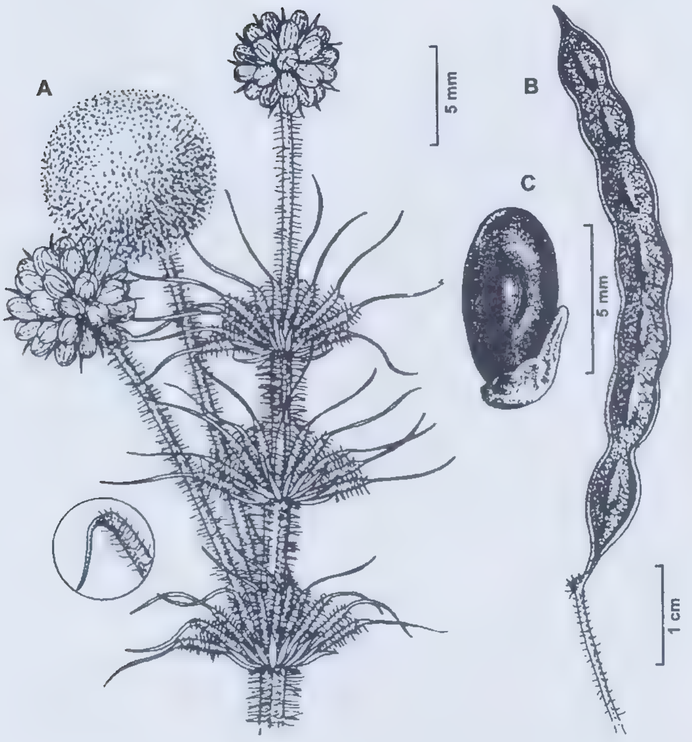

Figure 8. A-C, *Acacia smeringa*. **A**, portion of flowering branchlet with apex of phyllode (insert); **B**, pod; **C**, seed.

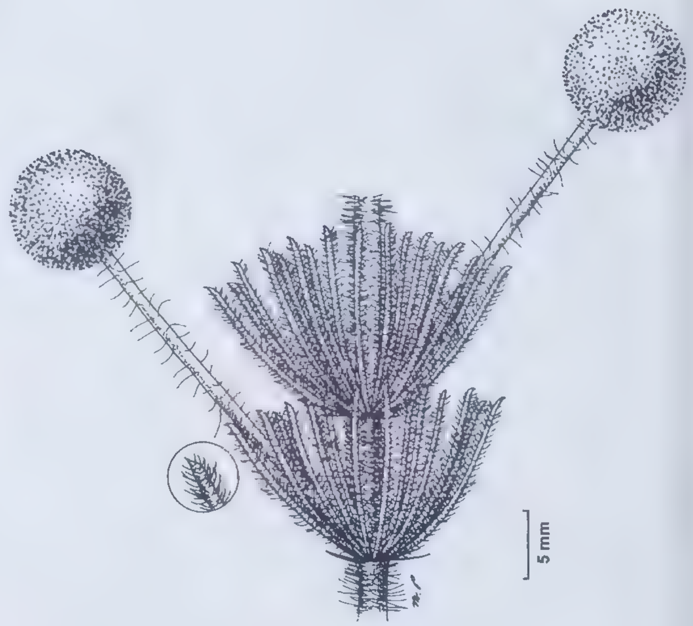

Figure 9. *Acacia zatrichota*. Portion of flowering branchlet with apex of phyllode (insert).

Prostrate *shrub* to ca. 1 m across, glabrous except sparse short hairs on stems and peduncles; internodes 5–28 mm long. *Phyllodes* 6–9 per whorl, spreading to ascending, uncinate with mucro 0.2–0.5 mm long, terete with 1 adaxial and 2 abaxial grooves, commonly 8–16 mm long; stipules subulate, 1.5–2 mm long, erect. *Peduncles* 13–37 mm long, glabrous. *Heads* commonly 20–25-flowered; bracteoles narrowly lanceolate, acute, ca. 2 mm long, glabrous. *Calyx* 0.5 mm long; lobes triangular with prominent midrib. *Corolla* 2.5 mm long, striate throughout. *Pod* stipitate, 1.5–5 cm long, 4–5 mm wide, ?glabrous; margin slightly thickened. *Seeds* (not seen mature) 4–7 per pod, longitudinal; pleurogram obscure; aril oblique, boat-shaped.

Distribution and habitat Known from the type locality in the Kimberley, WA (Fig 7), where it is common on a steep sandstone hillside with spinifex (*Plectrachne*) and shrubland, and from Jasper Gorge, NT, also growing in sandstone. Flowers in March.

Conservation status 1K-

Etymology The specific epithet is from the Latin *repens* (creeping), in reference to the unusual habit.

Other collection examined Jasper Gorge, W of Jasper Creek on road to Timber Creek, NT, *B R Maslin 7485, M McDonald & G Leach* (DNA, PERTH).

Affinities Foliage bright green; branches purplish. Distinguished by the prostrate habit which it shares with *A. hypermeces* but from which it differs in the sparse indumentum on branches and peduncles only, the fewer phyllodes per whorl, a shorter uncinate mucro on the phyllodes, the prominently striate corolla and a much shorter stipe to the pod. The Jasper Gorge collection is more hairy than the type but otherwise is a reasonable match.

Acacia smeringa A S George, sp nov (Fig 8 A-C)

Ad *Acaciam lycopodiifoliam* Cunn ex Hook affinis, a qua phyllodiis in quoque verticillo 15–20; phyllodiis recurvis ad uncinatis mucrone longissimo (2.5–3 mm longo); pedunculis longioribus (14–22 mm longis); calyce longiori (1.5 mm) lobis brevibus latis; et corolla glabra vix striata, differt.

Typus: Packhorse Range, WA, ca. 16°3', 125°6', May 1905, *W V Fitzgerald 1009* (holo: PERTH 00187143).

Erect *shrub* to ca. 1 m tall. *Stems* loosely tomentose with white hairs to ca. 0.5 mm long; internodes 5–15 mm long. *Phyllodes* 15–20 per whorl, erect to spreading with recurved to uncinate tip, linear, thick, 2–7 mm long, setose; mucro 2.5–3 mm long, excentric, spreading to recurved, glabrous; stipules linear-subulate, 1.5–2 mm long, incurved, yellowish. *Peduncles* 14–22 mm long, pilose with spreading white hairs. *Heads* ca. 30-flowered; bracteoles lanceolate, subulate, concave, 2–2.5 mm long, glabrous, the margins slightly irregular. *Calyx* 1.5 mm long, shortly broadly and obtusely lobed, ribbed, glabrous. *Corolla* 2.5 mm long, scarcely ribbed, glabrous. *Pod* sessile or almost so, linear, gently curved, flat but raised over seeds, 3–7.5 cm long, 5–6.5 mm wide, glabrous, brown; margin thickened. *Seeds* 5–9 per pod, longitudinal, ovoid-obovoid with oblique apex, 5–6 mm long, 3.5 mm wide, black, shining; pleurogram elliptic-obovate, closed, 1 mm long; aril boat-shaped along seed, 3–4 mm long; funicle small.

Distribution and habitat Known from the type, a collection from near Mt Jameson, and one from near the Manning River, WA (Fig 7). Grows in shallow rocky soil, in woodland dominated by *Eucalyptus argillacea* with *Plectrachne* common in the understorey. Flowers in May–June.

Conservation status 2K-

Etymology The specific epithet is taken from the Greek *merinx/smerinx* (a bristle), in reference to the bristly aspect of the plant due to the long mucro of the phyllode.

Other collections examined near Manning River, *I Cowie 329* (PERTH); Mt Jameson area, *E R Tudor B14* (MEL).

Affinities Related to *A. lycopodiifolia* Cunn ex Hook but distinguished especially by the recurved to uncinate phyllode tip with very long mucro, the more numerous phyllodes per whorl, longer calyx with short, broad lobes, and glabrous, scarcely striate corolla. The phyllode shape, shortly lobed calyx, larger scarcely striate glabrous corolla and closed pleurogram distinguish it from *A. capillaris*. The collection from the Mt Jameson area is very close to the type morphologically but has a mucro on the phyllode only 1.5–1.7 mm long. A recent collection from the Caroline Range, *R L Barrett 619* (PERTH), closely resembles *A. smeringa* but has hispid flowers.

Acacia zatrichota A S George, sp nov (Fig 9)

Inter species alias sect *Lycopodiifoliae* indumento densissimo, phyllodiis grandibus (8–18 mm longis), capitulis grandibus, bracteolis et calyce glabro, praecipue differt.

Typus: above Picaninny Gorge, Bungle Bungle National Park, WA, 17° 26' S, 128° 24' E, 4 July 1989, *K A Menkhorst 475* (holo: PERTH 1582586; iso: DNA, MEL).

Erect *shrub* to 1.5 m. *Stems* densely pilose with white hairs; internodes 2–9 mm long. *Phyllodes* 16–20 per whorl, erect, straight to incurved, terete, obscurely 1-grooved adaxially, 8–18 mm long, with an oblique mucro 0.2–0.4 mm long, pilose with spreading yellowish hairs; stipules subulate, 0.5–2.8 mm long, spreading, brown. *Peduncles* solitary, 23–30 mm long, sparsely pilose with white hairs. *Heads* ca. 30-flowered; bracteoles lanceolate, acuminate, 2.5–3 mm long, glabrous. *Calyx* 0.7–0.8 mm long, with short narrow lobes, smooth, glabrous. *Corolla* 2.5–2.8 mm long, glabrous except hirsute, smooth to faintly striate lobes. *Pod* sessile, linear, not viscid, not seen mature. *Seeds* 3–6 per pod, ?longitudinal, not seen mature.

Distribution and habitat Occurs in the Bungle Bungle National Park, south-eastern Kimberley, WA (Fig 7). Grows in dissected sandstone, with open woodland or shrubland usually with *Triodia*. Flowers in June–July.

Conservation status 2KC-

Etymology The specific name is from the Greek *trichotos* (hairy) with the intensive participle *za-* used as a prefix, in reference to the prominent indumentum.

Other collections examined Bull Ck, Bungle Bungle National Park, *G N Cowie 924* (DNA); Swamp Creek, Winnama Gorge, *S J Forbes 2527* (BRI, MEL).

Affinities A distinctive species with large hairy phyllodes and large heads. The glabrous bracts and calyx are characteristic.

Acknowledgments: Part of this work was carried out while I was employed by the Australian Biological Resources Study in Canberra; I greatly appreciate the support of that organisation, and of Helen Hewson in particular. It was completed at the Western Australian Herbarium, where I gratefully acknowledge the assistance of Bruce Maslin, Stan Webster and the late Richard Cowan. The Directors of the Australian National Herbarium, Northern Territory Herbarium and the Queensland Herbarium kindly made available material on loan. Collections at the National Herbarium of Victoria and the Royal Botanic Gardens, Kew, were examined during my visits to those institutions. Margaret Pieroni, Attadale, WA, prepared the illustrations, some of which were funded by ABRS for publication in the 'Flora of Australia'.

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Aprasia picturata (Squamata: Pygopodidae), a new legless lizard from the interior of Western Australia

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Abstract

A new species of pygopod, *Aprasia picturata* is described from the arid interior of Western Australia. The two specimens of the new species are from stony terrain near Leonora about 250 km from Bungalbin sandplain where the nearest *Aprasia* (*A. repens*) has been collected.

The head scalation of the new species is most like *Aprasia rostrata*, the colouration most like *Aprasia smithi*.

Introduction

The 35 species and eight genera of legless lizard (Pygopodidae) currently recognised are confined to Australia and New Guinea. Of these, 34 species and all eight genera occur in Australia (Cogger 1992) and in New Guinea there is one genus and two species (Kluge 1974). In Western Australia there are 23 species and six genera of pygopods (Storr *et al.* 1990). The monotypic genera *Aclys* and *Pletholax* and eight of the 10 known worm-like fossorial species of *Aprasia* are only found in Western Australia and then, almost exclusively, along the coast. In Western Australia, members of the genus *Aprasia* are found on Hermite Island in the north and on the mainland from North West Cape south and east to Esperance and the southeast coast east of the vicinity of Toolina Rockhole (Fig 1). Even *A. repens*, which occurs as far inland as Lake Magenta (33° 27′ S, 119° 11′ E) and the Bungalbin sandplain (30° 17′ S, 119° 45′ E), where an isolated population occurs, is most common on the Swan Coastal Plain.

The first specimen of the new species described below was collected by J Henry while carrying out an environmental assessment of a mining lease in the eastern goldfields of Western Australia. Its habitat is unusual for an *Aprasia* in that it is in the arid interior, often dominated by mulga (*Acacia aneura*) on stony, loamy soil (Fig 2). Furthermore, its colouring is unique; on the back it is rich orange-brown rather than being sombre grey or light or pale brown like other members of the genus.

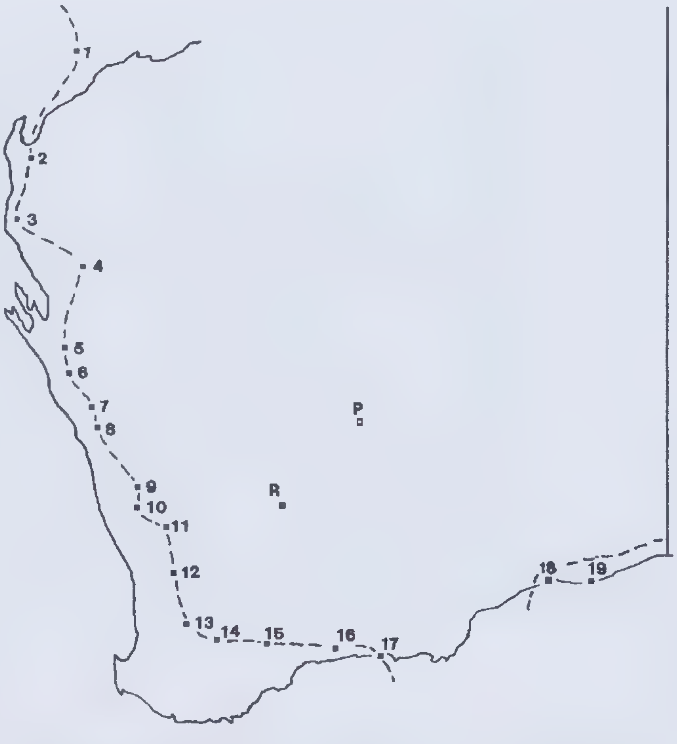

Figure 1. Southern portion of Western Australia showing the distribution of *Aprasia* in Western Australia. Dotted line indicates the inland limits of *Aprasia* species in Western Australia; the numbers the most inland records for various species :1 (*A. rostrata* Hermite I.), 2 (*A. fusca* Bullara), 3 (*A. fusca* 9 km E Point Cuvier), 4 (*A. smithi* Towrana), 5 (*A. smithi* Nerren Nerren), 6 (*A. smithi* 46 km N Galena), 7 (*A. smithi* East Yuna Reserve), 8 (*A. repens* Eradu), 9 (*A. repens* 15 km N Marchagee), 10 (*A. repens* Coomberdale), 11 (*A. repens* Wongan Hills),12 (*A. repens* York), 13 (*A. repens* Lomos), 14 (*A. repens* Dumbleyung), 15 (*A. repens* Lake Magenta), 16 (*A. repens* Oldfield River), 17 (*A. repens* Esperance), 18 (*A. inaurita* Vicinity of Toolina Rockhole), 19 (*A. inaurita* Middini Beach). "R"indicates the Bungalbin sandplain population of *A. repens* and "P" the *A. picturata* localities.

Systematics

Aprasia picturata sp nov

Holotype

R126998 an adult male collected 35 km E of Leonora in latitude 28° 57′ 15″ S, longitude 121° 47′ 23″ E by J Henry on 3 October 1996.

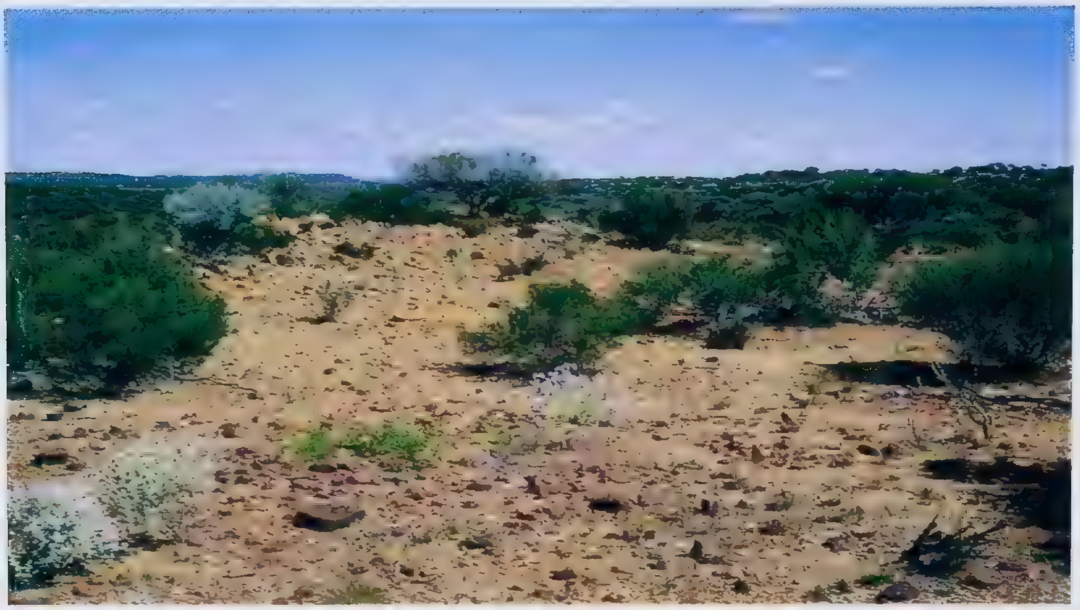

Figure 2. Habitat of *A. picturata* paratype photographed by B Maryan.

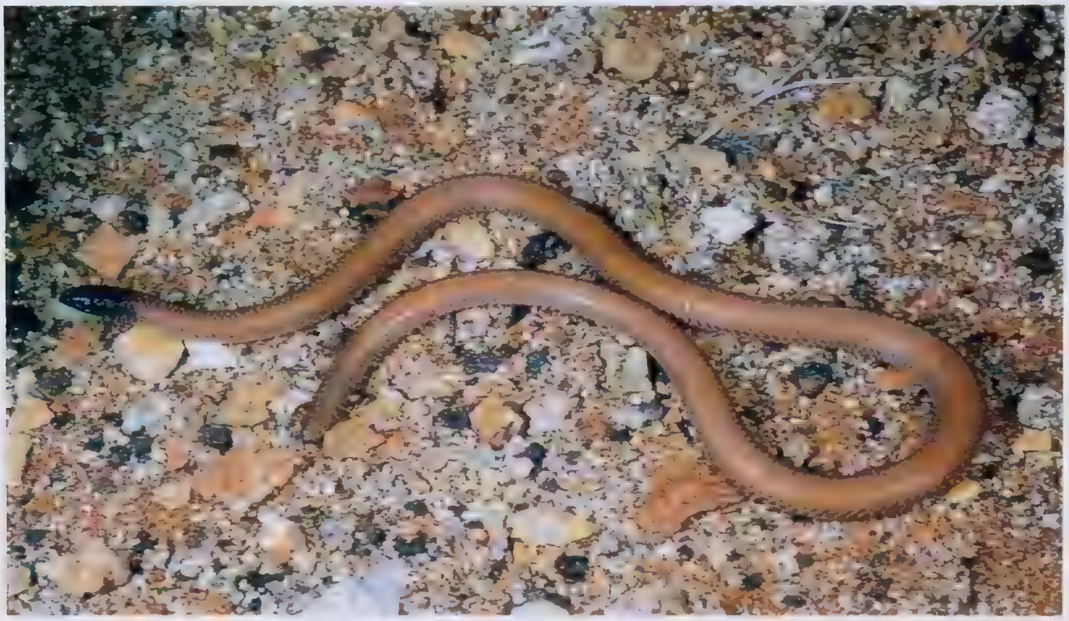

Figure 3. Paratype of *A. picturata* in life photographed by B Maryan.

Paratype

R131647 collected 3.5 km S of Minara HS in latitude 28°27′ 00″ S, 121°48′ 00″ E by B Maryan, G Harold and M True on 3 September 1997.

Diagnosis

In colouration *Aprasia picturata* is most like *Aprasia smithi* in having a black head but differs from it by lacking white lips and a black tip to the tail and having a rich orange-brown rather than yellowish-brown back (Fig 3). With five upper labials, a postocular (albeit small), 14 midbody scale rows and the first labial fused to the nasal anterior to the nostril *A. picturata* is most like *A. rostrata* (Table 1). Both species also have a beaked rostral but *A. rostrata* is pale brown on the back.

Table 1

Number of midbody scales rows and number and condition of upper labials in Western Australian *Aprasia* species.

Species	Upper labials	Midbody scale rows	Postocular free	First labial partly fused to nasal
fusca	5	14 (sometimes 12)	No	Yes
haroldi	4	14	No	Yes
inaurita	5	14	Yes	Yes
picturata	5	14	Yes	Yes
pulchella	5	14	Yes	No
repens	5	12	No	Yes
rostrata	5	14	Yes/No	Yes
smithi	5	12	No	Yes
striolata	5	12	Yes	Yes

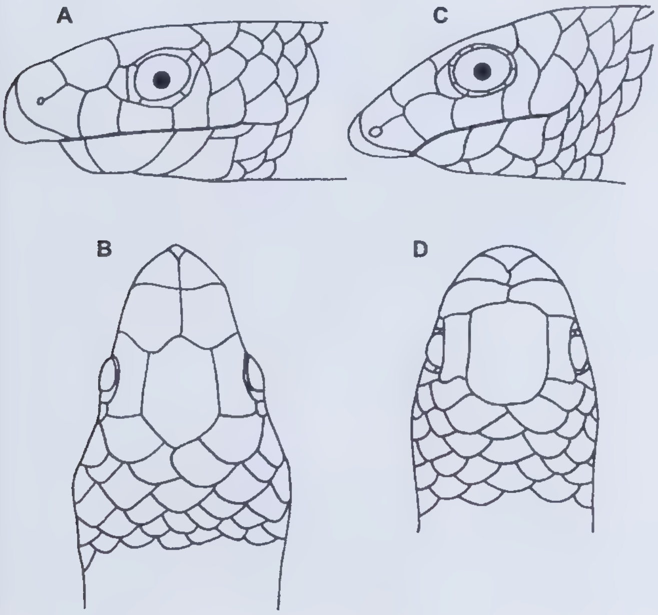

Figure 4. Head of holotype of *Aprasia picturata* (A & B) and head of *Aprasia smithi*, WAM 64350 (C & D). The small, shallow third lower labial is present on both sides of both specimens of *A. picturata*.

Description

Snout-vent length of holotype 122 mm, tail 97 mm (85% of SVL); SVL of paratype 143 mm, tail damaged.

Rostral barely visible from above, beaked in profile (Fig 4). Prefrontal in equal contact with first and second labials. One preocular. One postocular. Five upper labials, first anteriorly fused to nasal, the fourth high but separated from the supraocular by the postocular. Parietals fragmented. Midbody scale rows 14.

Top of head back to four nuchals beyond the parietals black, the black gradually merging with the orange-brown of the back. Mental and infralabials brownish-black. Eleven gular scales behind the mental particoloured (anterior half. dark brown, posterior half brownish white). Back rich orange-brown in life (pinkish -brown in alcohol) with four weak, interrupted brown streaks which continue onto the yellowish-brown tail. Tip of tail freckled black. Lateral scales smudged brown, smudges on each scale tending to align in 2-3 lines. Ventrals smudged brown, subcaudals less so.

Distribution

Two sites in close proximity in the arid interior of southern Western Australia (Fig 1).

Habitat

The holotype was pit-trapped on the crest of a low rocky greenstone ridge with small pockets of sandy loam. The surrounding vegetation comprised a shrubland of *Acacia aneura, A. burkittii, A. stowardii,* and *A. ramulosa* over mixed low shrubs and grasses. The paratype was collected from under a rock on a low rocky ridge with sparse *Acacia* and *Eremophila* shrubs (Fig 2).

Remarks

The testes of the male holotype are turgid (7.1 and 6.8 mm long). The paratype is a female.

Etymology

The specific epithet *picturata* (Latin for 'painted') alludes to the bright colour of this species compared with other *Aprasia*.

Acknowledgements: We are grateful to PC Withers, University of Western Australia, for his unpublished records from the Bungalbin sandplain where seven specimens of *A. repens* were trapped in 1992 and one in 1995. We also thank B Maryan, G Harold, G Barron and M Peterson for their enthusiasm and persistence which led to the collection of the paratype. B Maryan also provided the photographs for figures two and three. R Johnstone assisted with figure four.

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Water chemistry of the wetlands of the Yellagonga Regional Park, Western Australia.

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Abstract

Yellagonga Regional Park was established in 1989 as an area of significant value for conservation and recreation. Its wetlands include Lake Joondalup, Lake Goollelal and Walluburnup and Beenyup Swamps, which together are an important community resource both scientifically and recreationally. We investigated the water chemistry of the Yellagonga Park wetlands over a 15-month period, based on fortnightly sampling from five wetland areas. All the wetlands in the Park can be described as eutrophic on the basis of their phosphorus and nitrogen levels. However, analysis of the physico-chemical data identified two site clusters, each with distinctive chemistries. Beenyup Swamp and the southern end of Lake Joondalup were separated from the remaining sites on the basis of their very high phosphorus levels, and their lower levels of nitrogen, chlorophyll *a*, dissolved oxygen, pH and conductivity.

Nitrogen is likely to be a limiting nutrient in the highly P-enriched waters and this, together with the strongly alkaline pH of these wetlands makes them particularly susceptible to blue-green algal blooms of increasing intensity. Substantial phytoplankton responses in Beenyup Swamp were not evident during this study, despite this wetland having the highest phosphorus loadings. It is suggested that the presence of humic substances in this well-vegetated wetland, either directly or indirectly, ameliorated the primary productivity response to the enrichment. These wetlands exhibit strong seasonal variations in conductivity and ion concentrations, and relatively high mean values for these parameters are an established feature.

The outcomes of the study have implications for the long-term management of the Yellagonga Regional Park's wetlands, which needs to address the prevention of further deterioration in water quality and the restoration and conservation of the wetland and riparian habitats.

Introduction

The Yellagonga Regional Park, in the north-west corridor of Perth, contains some of the most important wetlands of the Swan Coastal Plain which comprise, in a north-south direction, Lake Joondalup, Beenyup Swamp, Walluburnup Swamp and Lake Goollelal (Fig 1). The Park covers an area of approximately 1400 ha, of which the wetlands make up about 550 ha. These wetlands are surface expressions of the unconfined aquifers of the Gnangara Mound, and provide some of the largest permanent sources of freshwater remaining on the Swan Coastal Plain. The groundwater inflow, which supplies the Yellagonga wetland system, is from shallow aquifers of up to 50 m in depth, flowing in an east to west direction towards the Indian Ocean.

Water levels in all the wetlands fluctuate on a seasonal basis in response to rainfall, evaporation, groundwater movement, and as a result of surface water flow between them. Lake Goollelal and the main water body of Lake Joondalup usually retain water over the dry summer periods whereas Beenyup Swamp and the southern end of Lake Joondalup are seasonal. This latter wetland area is separated from the main water body of Lake Joondalup by Ocean Reef Road and an engineered tunnel passing underneath Ocean Reef Road connects the two waterbodies. Surface water flows from the southern region into the main water body when water levels are sufficiently high, during the winter months.

The soils (McArthur & Bettenay 1974) and vegetation of the Park (Beard 1979) have been well described. The wetlands and their surrounds are of cultural, historical as well as faunal (avian) significance (Bekle 1979) and the establishment of the area as a Regional Park in 1989 reflected its importance for both conservation and recreation. The Yellagonga Regional Park is situated in an area of intense and growing urbanisation and, like others on the Swan Coastal Plain, the wetlands are increasingly threatened by eutrophication and degradation. Large areas of land have been cleared for agricultural and recreational purposes and the Park is influenced by the impact of increasing numbers of residential dwellings, and a range of land uses including market gardens and parkland. The water quality of the wetlands is increasingly influenced by urban drainage, stormwater flows, pollution, excessive nutrient input and groundwater extraction.

Previous studies of the nutrient status of these wetlands focussed on Lake Joondalup, the largest and

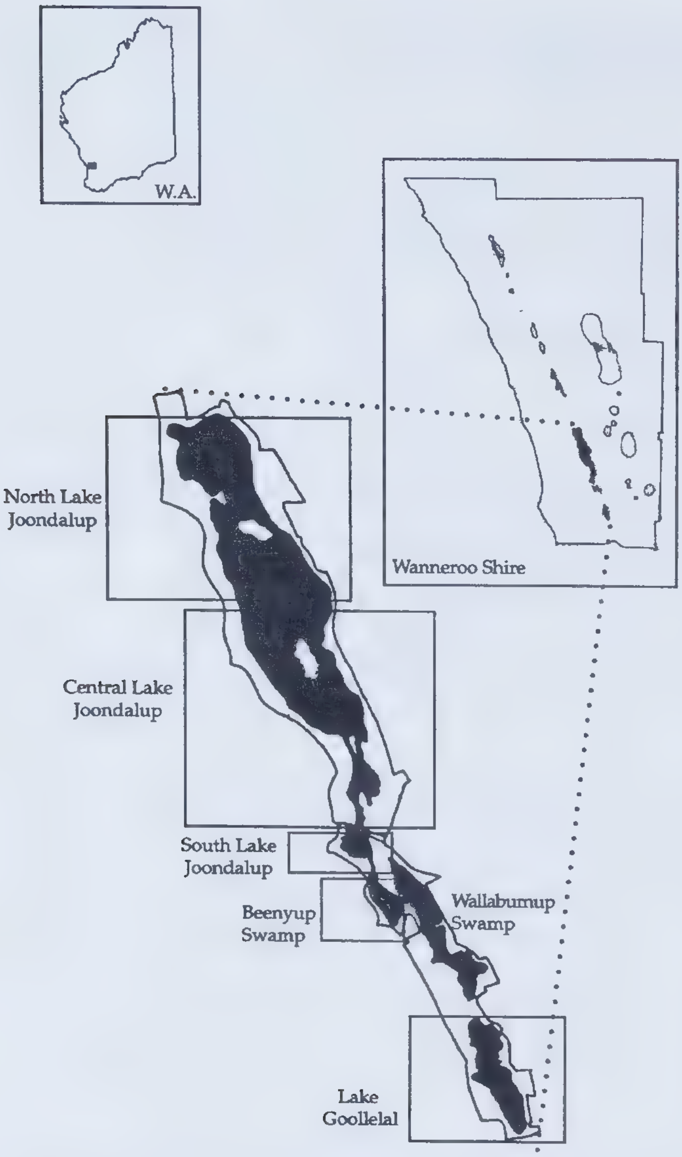

Figure 1. The major wetlands in the Yellagonga Regional Park and the locations of the five sampling areas of this study.

most visually dominant wetland in the park. The first study of Lake Joondalup (Congdon & McComb 1976) described the lake as "mildly eutrophic" on the basis of its phosphorus and nitrogen concentrations. Ten years later, the lake was described as excessively eutrophic by Congdon (1986), who concluded that substantial phosphorus enrichment was probably occurring via surface flow from Walluburnup/Beenyup Swamp. Davis *et al.* (1993) described the main water body of Lake Joondalup as mesotrophic.

This paper describes the seasonal and spatial patterns in selected aquatic physico-chemical characteristics of the three major wetlands within the Yellagonga Regional Park, Lake Joondalup, Beenyup Swamp and Lake Goollelal. The outcomes provide baseline water chemistry data for each of the wetlands as well as providing a "third decade" of water chemistry values for Lake Joondalup, providing an opportunity to identify any significant trends as a result of sustained anthropogenic loadings over the last two decades.

Methods

Site descriptions

Lake Joondalup is a large permanent wetland approximately 450 ha in area. Large sections retain the natural fringing vegetation of *Melaleuca raphiophylla* and sedges and two central islands are surrounded by sedge habitat. Eighty percent of the lake's area has a depth of 1.2-2.0 metres. A rich benthic flora and a suspended "sediment" of unknown origin called metaphyton (Rose 1979) inhabits the northern lake areas. The southern section of this wetland, south of the bisecting highway is seasonal, and dries out during summer. Beenyup Swamp is the smallest and shallowest water body of the three wetlands and dries out completely during the summer months. Most of the fringing vegetation has been retained and the swamp is heavily shaded throughout by *Melaleuca* sp. Lake Goollelal is a permanent wetland of approximately 50 ha. Its surrounds are heavily urbanised and it retains only a very small proportion of the natural fringing vegetation.

Previous studies had identified somewhat different chemical and botanical characters for the extreme southern and northern regions of Lake Joondalup. For example, the southernmost end of this lake is seasonal, has little benthic flora and has been described as excessively enriched (Congdon 1986). On the other hand, the deeper main water body is permanent, has been variously described as mesotrophic or mildly eutrophic, is known to support a rich benthic flora and has a suspended sediment called metaphyton distributed throughout the water column (Rose 1979). The road and sub-surface drain between the southern end of Lake Joondalup and the remaining part of this water body interrupts the natural lake contours and the south-north drainage. For these reasons, Lake Joondalup was divided into three sampling areas designated South, Central and North Lake Joondalup (Fig 1). Each of these areas was sampled separately and the data analysed as such, giving, with Beenyup Swamp and Lake Goollelal, a total of five sites in all.

Sampling and water analysis

Replicate water samples were taken at each of the five sites at two-weekly intervals for 15 months, commencing in January 1992. Conductivity, dissolved oxygen, temperature and pH were measured *in situ* at approximately 30 cm below the surface and near the centre of each water body, using Orion portable meters, after calibration. Water levels of both Lakes Joondalup and Goollelal were measured on all sampling occasions at the Western Australia Water Authority sites.

Water samples for the remaining analyses were transported to the laboratory over ice. Analyses for sodium, potassium, magnesium and calcium followed standard procedures for atomic absorption spectrophotometry (Clesceri *et al.* 1989). Chloride was measured by a modified argentometric method using a Corning 926 chloride analyser. Total alkalinity was determined by titration with HCl (Clesceri *et al.* 1989) and is expressed as mg $CaCO_3$ L^{-1}.

Samples for nutrient analyses were filtered through 0.45 µm filters and stored frozen until analysed. Nitrate/

nitrite was determined spectrophotometrically following cadmium reduction (Clesceri *et al.* 1989). Ammonium nitrogen was determined by the formation of indophenol, detected spectrophotometrically (Grasshof *et al.* 1983). Organic nitrogen was determined by the difference between Kjeldahl nitrogen and ammonium nitrogen. Kjeldahl nitrogen was determined by digestion followed by spectrophotometric analysis of the ammonia produced (Clesceri *et al.* 1989). Total nitrogen was obtained by summing ammonium nitrogen, organic nitrogen and nitrate/nitrite.

Filterable reactive phosphorus was determined spectrophotometrically by the single solution (ascorbic acid) method (Major *et al.* 1972). Total phosphorus (filterable reactive phosphorus, condensed inorganic phosphate and organic phosphate) was determined by the same method following digestion with perchloric acid using a block digester.

Chlorophyll *a* was used as an indicator of algal biomass (phytoplankton productivity). Chlorophyll *a* was determined spectrophotometrically following extraction from the glass fibre filter paper by grinding with acetone (Clesceri *et al.* 1989).

Data analysis

The site data for each of the variables were converted to monthly mean values for identifying broad-scale seasonal patterns and environmental gradients. These gradients were further summarised as tabulated single mean values and ranges for each of the chemistry variables for each site. For identification of overall trends in the data set, classification and ordination of the 5 sites were carried out using the seasonal mean values (5 seasons in all) of seven variables, total nitrogen, total phosphorus, filterable reactive phosphorus, chlorophyll *a*, pH, dissolved oxygen and conductivity. The procedures for classification and ordination of the data followed those recommended in the PATN software package (Belbin 1989). The data were log-transformed and standardised by range. The association between pairs of mean values was estimated using the Gower Metric Association measure. To classify the samples, a hierarchical clustering strategy (FUSE) was used to identify and group the pair of samples which were most closely associated. An arithmetic averaging strategy (UPGMA) was then used to create a new association value between the newly-grouped samples and all other samples. This process was iterated until all samples had been grouped to produce an agglomerative cluster pattern. The resulting dendogram is the graphical representation of this successive fusion of samples within groups, based on the original association values.

Ordination is a complementary technique to classification and has the objective of condensing the information in the data set so that the patterns can be displayed in only two or three dimensions. The samples were ordinated using the recommended semi-strong hybrid multidimensional scaling strategy (SSH) in PATN (Belbin 1989). When plotted in this limited number of dimensions, the similarity between the samples is measured by the plot-distance between them. Most similar samples are closest together, those most dissimilar are furthermost apart. The "stress value" can be used as an indication of how well the arrangement of the samples in the low-dimension space reflects the among-sample relationships in the original multi-dimensional data set. An ordination with a stress value of <0.05 is considered to provide an excellent representation, with little danger of misinterpretation (Clarke 1993).

Results

The commencement of sampling occurred in the summer of 1991/1992, when abnormally high rainfall fell in both December and February (Fig 2). As a result of this summer rain, the normally seasonal wetland areas, South Lake Joondalup and Beenyup Swamp retained water throughout the summer/autumn period of 1992 and the hydrographs for Lakes Joondalup and Goollelal show a slower decline in water levels prior to the winter of 1992 (Fig 3). The hydrographs also emphasise the strong

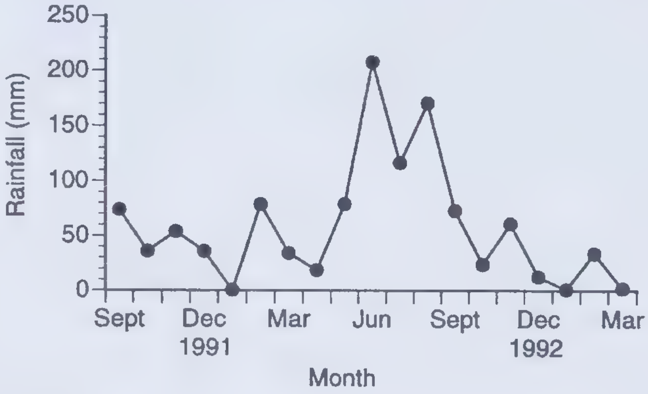

Figure 2. Monthly rainfall in Wanneroo during the period of the study (source: Wanneroo Station, Bureau of Meteorology, Perth).

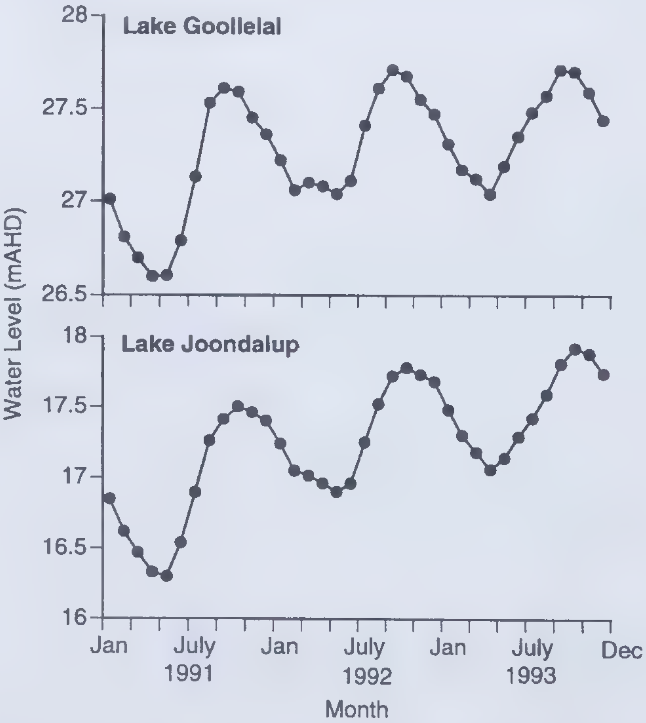

Figure 3. Hydrograph water levels for the Yellagonga wetlands for the period 1991-1993 (source: Western Australian Water Authority, Perth).

seasonal patterns in water levels occurring in these wetlands, a pattern which was reflected in the water chemistry.

Nutrient concentrations

Phosphorus: There were no obvious seasonal patterns in either total phosphorus (TP) or filterable reactive phosphorus (FRP) at any of the sites (Fig 4), but there was a clear gradient of increasing TP and FRP from north to south across the surface-connected Lake Joondalup/ Beenup Swamp sites (Table 1). Consistently high levels were recorded in Beenyup Swamp and South Lake Joondalup where values exceeded 100 µg L^{-1} for most of the sampling period. Monthly mean values approached the lower values of the northern Lake Joondalup areas only in the summer months of 1992/93. At these two southern sites, peaks in TP and FRP tended to parallel each other, with FRP usually contributing >60% of TP. In Lake Goollelal and Central and North Lake Joondalup, where TP and FRP values were considerably lower, there was increased variability in TP values after the onset of the winter rains, with small increases in the winter-spring months, particularly in Central Lake Joondalup. At these sites, the FRP contribution to TP was more variable and lower (generally <50%).

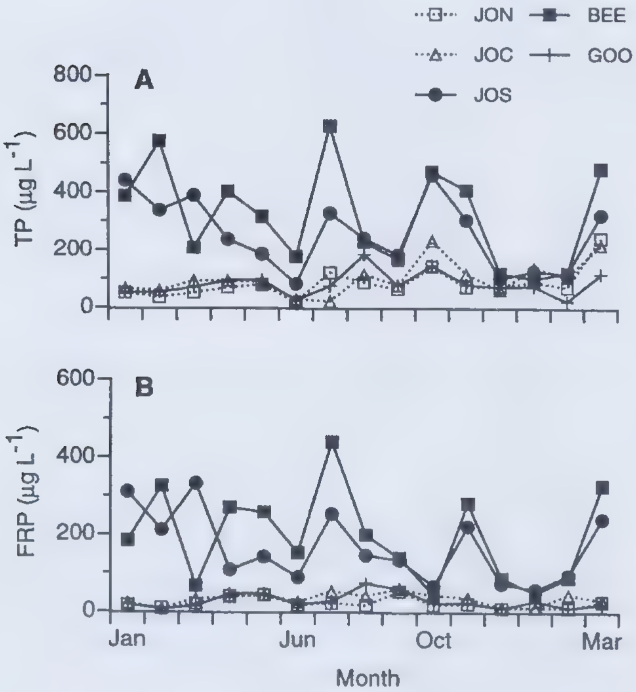

Figure 4. Variation in monthly mean phosphorus levels for North Lake Joondalup (JON), Central Lake Joondalup (JOC), South Lake Joondalup (JOS), Beenyup swamp (BEE) and Lake Goollelal (GOO). **A**: total phosphorus concentration (TP); **B**: filterable reactive phosphorus concentration (FRP).

Nitrogen: At all sites, organic nitrogen concentrations were almost always at least 90% of the total nitrogen values and spatial and seasonal patterns for these two variables were therefore identical. For this reason, ON values have not been included in Fig 5. The larger, permanent water bodies of Lakes Joondalup and Goollelal had the highest TN and ON levels and there were strong seasonal patterns, with maximum values around 3000 µg L^{-1} in summer/autumn, falling to minimum values around 1500 µg L^{-1} in late winter (Fig 5). Transient peaks in TN levels were recorded in Central Lake Joondalup in the spring and summer months.

In contrast, TN and ON levels in South Lake Joondalup rarely exceeded the minimum levels recorded at the other sites, and the only suggestion of a seasonal response was the transient high levels observed in South Lake Joondalup during the summer months.

Levels of inorganic nitrogen (both as nitrate/nitrite and ammonium nitrogen) were uniformly low on most sampling occasions across all the sites. One exception was Beenyup Swamp which maintained relatively high ammonium nitrogen levels (around 120 µg L^{-1}) throughout the unusually wet summer/autumn of 1992.

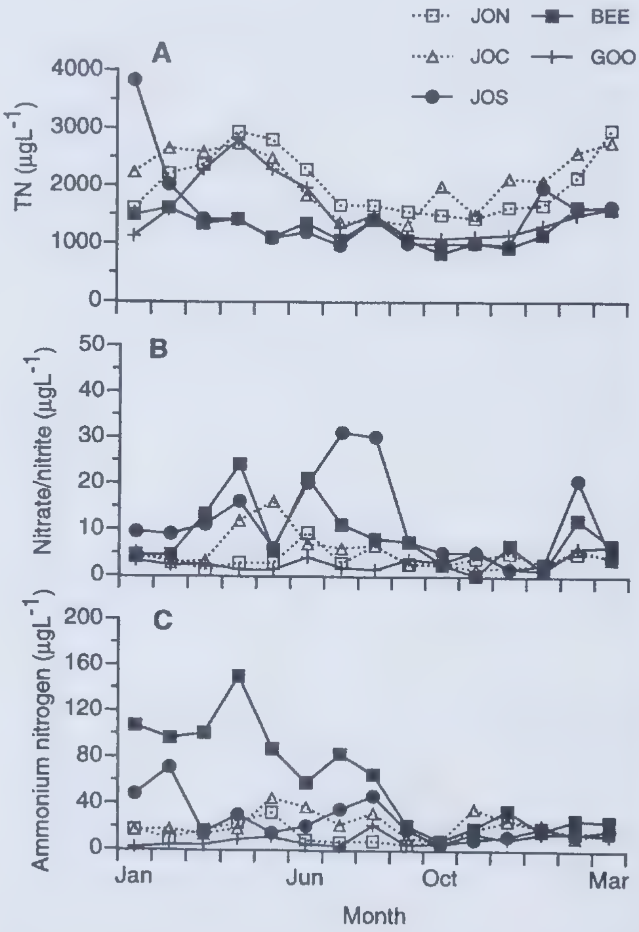

Figure 5. Variation in monthly mean nitrogen levels for North Lake Joondalup (JON), Central Lake Joondalup (JOC), South Lake Joondalup (JOS), Beenyup swamp (BEE) and Lake Goollelal (GOO). **A**: total nitrogen concentration (TN); **B**: nitrate/nitrite concentration; **C**: Ammonium nitrogen concentration.

Chlorophyll *a*

Chlorophyll *a* levels in the permanent water sites, North and Central Lake Joondalup and Lake Goollelal were maintained at levels consistently above 5 µg L^{-1} with some high monthly mean values (> 50 µg L^{-1}), particularly in Central Lake Joondalup (Table 1). Peaks in chlorophyll *a* which were recorded for the warmer spring/summer months in Central Lake Joondalup were associated with highly visible algal blooms (Fig 6). The most striking feature of the chlorophyll data from the remaining two sites, South Lake Joondalup and Beenyup Swamp, was the absence of a similar phytoplankton response to the higher observed phosphorus levels at these sites. In Beenyup Swamp, chlorophyll *a* levels were below 5 μg L^{-1} for most of the sampling period and levels here were the lowest for all the sites with no discernible peaks. In South Lake Joondalup, levels were also usually low during periods of south-to-north flow from the adjacent Swamp, but isolated high levels were observed in both summers and were associated with transient algal blooms.

Conductivity and ion concentrations

Conductivity values (Fig 7) and ionic concentrations showed similar, strong seasonal changes which reflected rainfall and evaporation patterns and consequent seasonal variations in water levels. For all these parameters, highest values occurred in late autumn and decreased rapidly with the onset of winter rains. The two sites comprising the largest water body (Central and North Lake Joondalup) showed the most pronounced

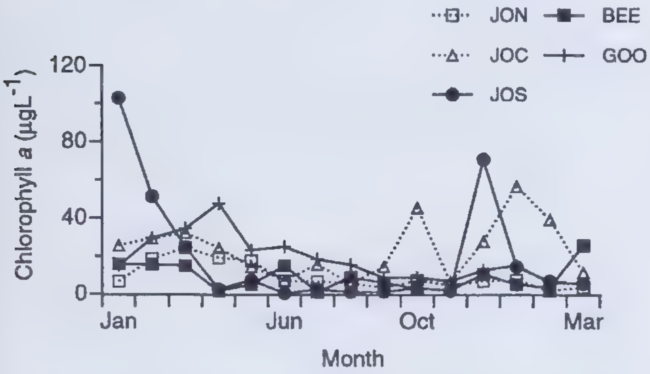

Figure 6. Variation in monthly mean chlorophyll *a* levels for North Lake Joondalup (JON), Central Lake Joondalup (JOC), South Lake Joondalup (JOS), Beenyup swamp (BEE) and Lake Goollelal (GOO).

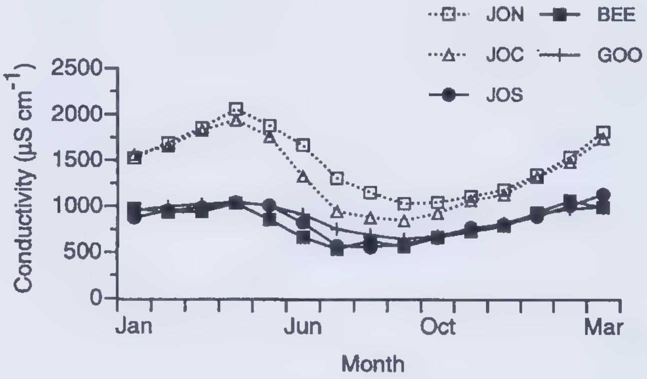

Figure 7. Variation in monthly means of conductivity for North Lake Joondalup (JON), Central Lake Joondalup (JOC), South Lake Joondalup (JOS), Beenyup swamp (BEE) and Lake Goollelal (GOO).

Table 1

Nutrient chemistry and chlorophyll *a* for the five sampled sites. Values are the means and ranges over the 15-month period.

SITE	Total Phosphorus (μg L^{-1})	Filterable Reactive Phosphorus (μg L^{-1})	Total Nitrogen (μg L^{-1})	Organic Nitrogen (μg L^{-1})	Nitrate/ nitrite Nitrogen (μg L^{-1})	Ammonium Nitrogen (μg L^{-1})	Chlorophyll *a* (μg L^{-1})
Lake	86	26	1507	1502	3	9	16
Goollelal	13-548	0-206	854-3018	882-3011	1-18	1-67	0-62
Beenyup	322	195	1257	1179	28	60	9
Swamp	80-831	25-689	760-1722	656-1725	1-328	8-185	0-37
South Lake	260	163	1425	1370	17	33	19
Joondalup	71-766	40-518	807-4002	791-3606	1-325	3-590	0-199
Central Lake	117	33	2134	2107	5	23	22
Joondalup	8-603	0-209	976-4515	818-4496	1-193	1-225	0-134
North Lake	88	23	2094	2078	4	15	10
Joondalup	9-555	0-218	1239-5901	1219-5883	1-44	1-54	0-31

Table 2

Conductivity, metal ions and chloride ions for the five sampled sites. Values are the means and ranges over the 15-month period.

SITE	Conductivity (μS cm^{-1})	Sodium (mg L^{-1})	Potassium (mg L^{-1})	Calcium (mg L^{-1})	Magnesium (mg L^{-1})	Chloride (mg L^{-1})
Lake	871	87	11	36	18	158
Goollelal	627-1054	45-154	4-16	20-52	13-24	168-218
Beenyup	816	85	6	46	14	149
Swamp	479-1096	50-127	4-9	26-67	9-19	85-212
South Lake	859	85	6	44	14	154
Joondalup	526-1190	54-147	5-8	27-64	9-19	98-216
Central Lake	1381	147	8	33	26	328
Joondalup	620-1977	50-233	2-17	18-47	11-46	132-598
North Lake	1501	160	8	29	29	360
Joondalup	980-2160	99-234	2-17	18-36	19-41	156-578

seasonal fluctuations. Noticeable in Fig 7 is the decrease in conductivity in Central Lake Joondalup in early winter as a result of seasonal water flow from South Lake Joondalup through the Ocean Reef Road culvert. With the exception of calcium, conductivity and ionic concentrations were highest in Central and North Lake Joondalup (Table 2). Calcium ion concentrations were highest in the southern end of Lake Joondalup and Beenyup Swamp.

Dissolved oxygen, pH and alkalinity

The alkaline pH values of the larger water areas (Table 3) would be expected from lakes overlying limestone formations. Values recorded for the small water body of Beenyup Swamp were near-neutral. Some seasonal variation was evident in three of the sites (Lake Goollelal, and South and Central Lake Joondalup) with higher pH values in summer. In South Lake Joondalup, we were able to associate the high pH values with high transient chlorophyll a values. Small seasonal variations were also observed in alkalinity with higher values in summer. This trend was more pronounced in the smaller water areas.

Both the spatial and temporal patterns in dissolved oxygen may reflect the sampling strategies. The shallow nature of Beenyup Swamp, particularly in the drier months, resulted in measurements close to sediments which may have contributed to the very low values. On the other hand, the deeper water bodies had relatively high values, indicative of well-aerated conditions in the surface layers, where these measurements were taken.

Multivariate analyses

The agglomerative clustering routine identified two clear interpretable site clusters which separated the Beenyup Swamp and South Lake Joondalup sites from the remaining sites (Fig 8). This site pattern was also obtained when the sites were ordinated over three dimensions, with the best separation occurring over axes 1 and 3 (Fig 9). The separation of the Beenyup and South Lake Joondalup sites by both clustering and ordination strategies reflects the combination of high mean levels of total and filterable reactive phosphorus, but low mean levels of total nitrogen, dissolved oxygen, pH and conductivity.

The classification and ordination procedures indicated some separation of S1, the wet summer samples from South Lake Joondalup. The water chemistry of this site during this period was distinctive because of the isolated but very high, transient chlorophyll *a* levels.

Table 3

Dissolved oxygen, pH and alkalinity for the five sampled sites. Values are the means and ranges over the 15-month period.

SITE	Dissolved oxygen (mg L^{-1})	pH	Alkalinity (mg L^{-1} $CaCO_3$)
Lake Goollelal	8.3 5.6-13.0	8.4 7.3-10.0	104 72-137
Beenyup Swamp	3.0 0.3-10.0	7.4 6.1-8.1	153 92-230
South Lake Joondalup	6.5 1.8-9.0	8.1 6.9-9.6	160 84-226
Central Lake Joondalup	8.2 5.0-13.0	9.0 7.5-10.1	129 102-179
North Lake Joondalup	8.8 4.9-13.3	9.3 8.2-9.9	124 75-166

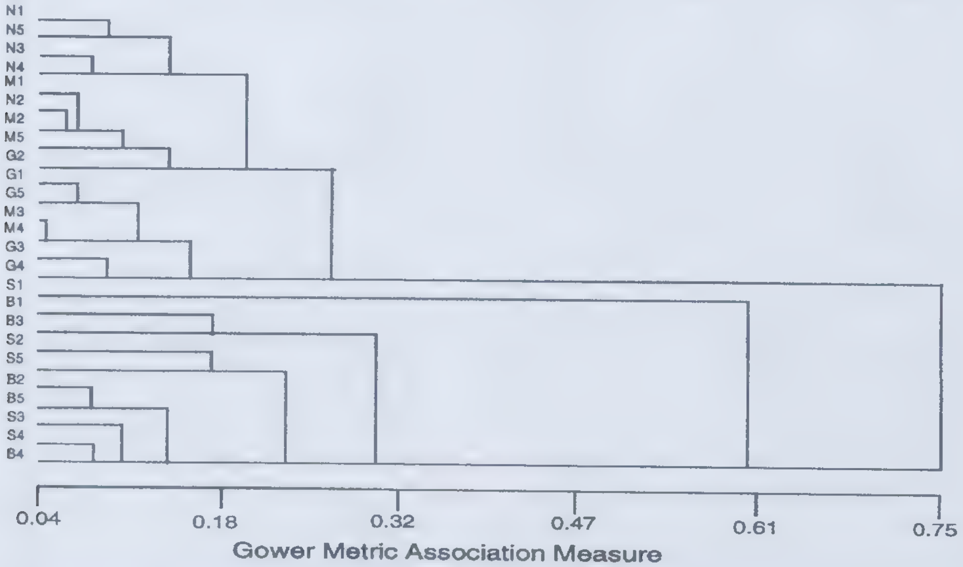

Figure 8. Hierarchical agglomerative clustering of water chemistry variables (TN, nitrate/nitrite nitrogen, ammonium nitrogen, chlorophyll *a*, pH, TP, FRP, dissolved oxygen and conductivity) of the five wetland sites sampled over five consecutive seasons, 1: summer/92 to 5: summer/93. (N=North Lake Joondalup, M=Central Lake Joondalup, S=South Lake Joondalup, B=Beenyup Swamp, G=Lake Goollelal).

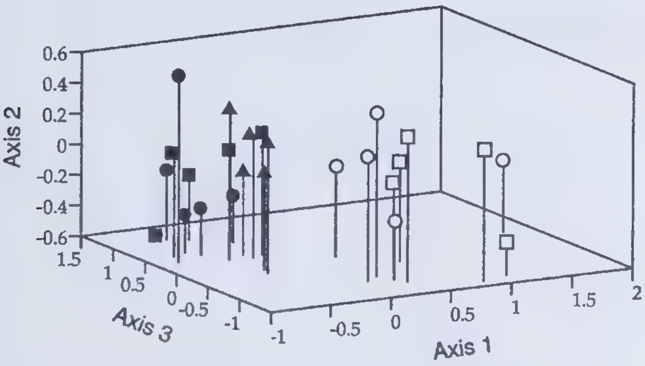

Figure 9. SSH ordination of selected water chemistry variables (TN, nitrate/nitrite nitrogen, ammonium nitrogen, chlorophyll *a*, pH, TP, FRP, dissolved oxygen and conductivity) of five wetland sites sampled over five consecutive seasons (summer/92 to summer/93). Seasonal means were ordinated over three dimensions. Stress = 0.046. (●=North Lake Joondalup, ■=Central Lake Joondalup, ○=South Lake Joondalup, □=Beenyup Swamp, ▲=Lake Goollelal).

Discussion

Our data describe temporal and spatial patterns in water chemistry in the Yellagonga Regional Park wetlands. Within the wetlands, temporal variations reflected seasonal changes in water levels. Across the wetland areas there were clear spatial gradients of nutrients.

The seasonal rainfall pattern and evaporation rates which result from our wet winters and hot dry summers were reflected in seasonal changes in conductivity, ionic concentrations, and total and organic nitrogen. These strong seasonal variations resulted from changes in the volume of water causing summer concentration due to low rainfall and high evaporation, and winter dilution due to high rainfall and increased water flow into the wetlands. Seasonal changes were particularly obvious for the largest wetland area comprising Central and North Lake Joondalup. Here, summer maxima were considerably higher than elsewhere, as a result of higher evaporation rates from the larger surface area.

The high conductivity and ionic levels are chemical features of these wetlands, with the mean conductivities corresponding to total dissolved salts of approximately 500 mg L^{-1} for Lake Goollelal, Beenyup Swamp and South Lake Joondalup and approximately 900 mg L^{-1} for Central and North Lake Joondalup (using a conversion factor of 1 $\mu S\ cm^{-1} = 0.64$ mg L^{-1}). These high levels reflect proximity to the coast with consequent precipitation of ionic salts from ocean spray (Congdon & McComb 1976). In addition, the wetland chemistry is likely to be influenced by groundwater inflow together with their location within the Spearwood Dune System and associated limestone formations. The conductivity and ion concentrations were somewhat lower than those of previous studies (Congdon & McComb 1976; Davis & Rolls 1987). This is likely the result of the higher summer rainfall in the Dec 1991/Feb 1992 and the subsequent higher water levels through 1992.

It is apparent from our study that the strong phosphorus gradients across the surface-connected areas of Lake Joondalup which were first identified by Congdon (1979) remain a feature of these wetlands. On the basis of the phosphorus and nitrogen levels the trophic status of all the wetlands in the Park can be described as eutrophic using either the CEPIS (Salas & Martino 1991) or OECD (1982) classification scheme for determining trophic category. In addition, our analysis of the nutrient ratios strongly suggests a relative increase in phosphorus in these wetlands over the last fifteen years (Table 4). Ratios of TN:TP decreased from 35:1 in 1978 to 21:1 in 1992. As well, IN:FRP ratios fell from 3.7 to 0.8 in the same period and suggest that nitrogen, rather than phosphorus, is now more likely to be the limiting nutrient for phytoplankton growth in these wetlands (Wetzel 1983). This, together with the naturally alkaline pH values renders these wetlands particularly susceptible to the formation of nitrogen-fixing blue-green algal blooms (Schindler 1977).

Table 4

Comparisons of total nitrogen (TN) : total phosphorus (TP) and inorganic nitrogen (IN): filterable reactive phosphorus (FRP) obtained from the main waterbody of Lake Joondalup from studies conducted over the last two decades (data from Congdon 1986; Davis & Rolls 1987; and the present study).

RATIO	1978	1979	1980	1985/86	1992/93
TN/TP ratio	35	30	35	47	21
IN/FRP ratio	3.7	1.6	1.9	1.5	0.8

The strong nutrient gradients that we have described across the length of Lake Joondalup define sites within the wetland with distinctive chemistries superimposed on the seasonal patterns. This was reflected by the results of the multivariate analysis which indicated a clear separation of Beenyup Swamp and South Lake Joondalup sites from the other wetland sites within Yellagonga Regional Park. These two sites had higher phosphorus levels, lower nitrogen and chlorophyll a levels and were less alkaline than the adjacent main water body of Lake Joondalup to the north and the geographically disjunct Lake Goollelal to the south.

The substantially higher nitrogen levels in the main water body of Lake Joondalup compared with the other areas, are due both to higher minima in winter (means of 1500 µg L^{-1} in the north compared with 1000 µg L^{-1} in the south) and higher maxima in the warmer months when water volumes are lowest. The higher overall mean values for organic nitrogen in the main water body of Lake Joondalup have two possible sources, one associated with phytoplankton blooms in summer/autumn and spring/summer, and a higher minimum value natural to this wetland which varies seasonally with water volume. Relatively high organic nitrogen values in the main water body of Lake Joondalup have been recorded previously (Congdon 1979; Davis & Rolls 1987) and Congdon & McComb (1976) suggest that this may reflect the release of nitrogen from the dense macrophyte vegetation and benthic hydrophytes that inhabit these areas. These vegetation communities are not as evident in the southern section of the lake.

The distinctiveness of Beenyup Swamp and to a lesser extent South Lake Joondalup was further enhanced by the presence of low chlorophyll *a* levels throughout much of the year, despite the higher phosphorus levels. Congdon (1986) recorded similar findings in the southern end of Lake Joondalup and suggested that factors other than nutrients may be limiting phytoplankton growth. Coloured wetlands are known to exhibit lower than expected algal growth under nutrient-enriched conditions (Wrigley *et al.* 1988). Lower pH due to acidic humic substances and reduced light penetration have both been suggested as possible reasons for this reduction in productivity. In Beenyup Swamp, it is likely that humic substances from this heavily-vegetated wetland contribute to the near-neutral pH in an otherwise strongly alkaline group of wetlands, and to the somewhat coloured water. However, gilvin levels of less than 16 g_{440} m^{-1} (Upton 1996) are not sufficiently high to describe this wetland as "highly coloured" if the criterion level of 52 g_{440} m^{-1} suggested by Davis *et al.* (1993) is used. The possible role of Beenyup water as an agent for ameliorating the effects of nutrient enrichment in the southern areas of this wetland complex highlights the importance of conserving vegetation and has implications for the future management of the wetlands.

The high dissolved oxygen levels in the surface water of the larger wetland sites are consistent with the relatively large surface area of the wetland system and its exposure to wind. Without more detailed measurements of dissolved oxygen, we are unable to comment on the degree of variation either diurnally or with depth in these wetlands. The very low levels of dissolved oxygen proximal to the sediments in the shallow water of Beenyup Swamp, particularly over the wet summer/autumn of 1992, may reflect enhanced microbial activity in these sediments, a suggestion supported by the relatively high levels of ammonium nitrogen. Depleted oxygen levels are also found in lakes that have high concentrations of humic compounds (Schmidt & Rosich 1993).

The presence of anoxic conditions above the sediments in the heavily-vegetated Beenyup Swamp has implications for the dynamics of sediment phosphorus and consequent management strategies. In shallow lakes with high concentrations of phosphorus in the sediments (as Congdon 1986, found for the sediments of Lake Joondalup), a sediment reservoir of labile organic material, anoxic conditions, and a high pH can each contribute to the release of phosphorus from the sediments. The subsequent internal load can then determine the trophic status of the wetland (Marsden 1989; Kleeberg & Kozerski 1997). In addition, air-drying of sediments from eutrophic lakes can induce significant increases in phosphate release, under both aerobic and anaerobic conditions (Qui & McComb 1994). Thus, it is possible that the regular drying of seasonal wetlands such as Beenyup Swamp and South Lake Joondalup may be followed by significant increases in internal phosphorus loadings when rewetting occurs. Efforts to restore shallow eutrophic lakes usually focus on reducing the external loading of phosphorus. However, this may not produce the expected reductions in phytoplankton biomass because of substantial internal loading of phosphorus from the sediments (Marsden 1989). Significant improvements to water conditions in such situations may take 5-10 years, if recovery occurs at all (Krienitz *et al.* 1996). This possibility has management implications for the Yellagonga wetlands.

Our study provides a seasonal and spatial picture of the water chemistry of the wetlands of Yellagonga Regional Park. The wetlands are strongly eutrophic, and the nutrient enrichment is resulting in visible algal blooms in the large water body of Lake Joondalup in the warmer months of the year. Whether absolute nutrient levels are increasing or not is difficult to determine due to the different sampling designs and analytical procedures used by researchers, as well as the varying rainfall and runoff patterns which influence lake fill and dilution effects both seasonally and annually. The unique character of Beenyup Swamp water may be ameliorating the effects of nutrient enrichment in the Swamp and, to a lesser extent, in South Lake Joondalup. It was not possible for us to provide definitive causes of the relatively low standing crop of phytoplankton in these sites and this aspect is worthy of further study.

Acknowledgments: The research was funded by the Edith Cowan University Foundation. The authors would like to thank S Medlock, M Bannister and V Pearmine for the field work and their technical expertise and assistance. The Western Australian Department of Conservation and Land Management provided the necessary licenses to carry out the work. We thank the reviewers for their helpful comments.

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ERRATUM

The legend to Figure 3 in Bayly (1999, Volume 81 Part 1) was inadvertently omitted; it was

Figure 2. A gnamma of the deep, pit-shaped variety on Pildappa Rock, a granite inselberg near Minnipa on the upper Eyre Peninsula, South Australia. This ovate gnamma measures 2.7 by 2.3 metres and has a depth of 70 centimetres.

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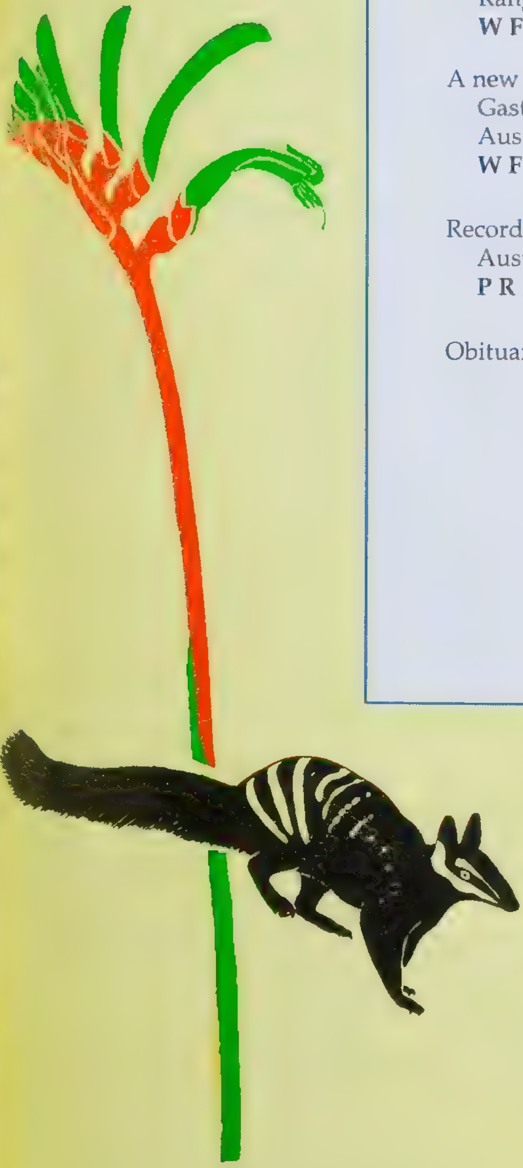

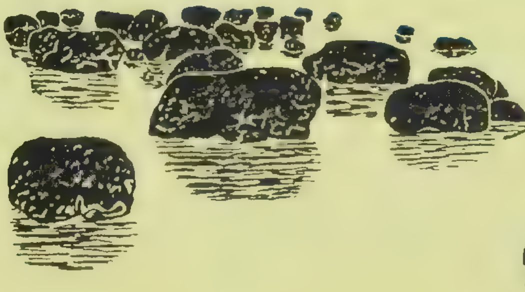

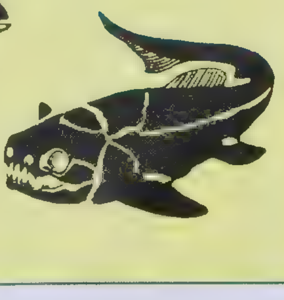

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Journal of the Royal Society of Western Australia, 82:89-98, 1999

Physico-chemical profile and energy fixation in Bundera Sinkhole, an anchialine remiped habitat in north-western Australia

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Manuscript received August 1998; accepted April 1999

Abstract

Bundera Sinkhole, in arid north-western Australia, contains a community of stygofauna, including remipedes and thaumatocypridid ostracods, whose closest known affinities lie with the fauna of anchialine caves on either side of the North Atlantic. The physico-chemical profile was determined using a sonde carried by divers and by chemical analysis. The physico-chemical profile is complex, as the characteristic thermo-halocline is associated with polymodal profiles of oxygen, hydrogen sulphide and redox to a depth of 33 m. Within the upper part of the profile there was a gradient in the dissolved inorganic nitrogen (DIN) species associated with the thermo-halocline, and an accumulation of NO_3 below the thermo-halocline that is consistent with nitrification, a chemolithotrophic process. The presence of sulphide layers above the thermo-halocline, together with characteristic colour and behaviour of the associated bacteria, are consistent with sulphide-based chemoautotrophy. Stable isotope ratios for carbon and nitrogen of the fauna and autotrophic energy sources are also consistent with chemosynthesis occurring in Bundera Sinkhole. The arid climate, low ground-water flow, and small size of the cave provides the stable conditions allowing the development of a marked polymodal vertical stratification in the physico-chemical profile. The input of profuse organic matter and the penetration of the photic zone to the thermo-halocline provide the varied conditions for the development of this complex microbiolgical assemblage.

Introduction

Anchialine (or anchihaline) ecosystems are inland underground mixohaline waters affected by marine tides, usually with little if any surface exposure (Stock *et al.* 1986; Iliffe in press). Anchialine systems are noted both for their relict faunas and their high species richness (Sket 1981, 1996); at least ten new families and a new class (the Remipedia) of crustaceans have been described from anchialine systems in the last few years (GA Boxshall, Natural History Museum, London, pers. comm.). Therefore they are the object of an accelerating research effort and widespread conservation assessment as their restricted, coastal warm latitude, often karstic, setting makes them exceptionally vulnerable to anthropogenic pressures, a theme developed more fully elsewhere (Humphreys *et al.* 1999).

Where anchialine systems occur in drowned sinkholes (cenotes), they typically have a freshwater layer overlying seawater and in consequence have a stratified photic and physico-chemical profile. The marine influence typically consists of an hypoxic layer of seawater (*ca.* 33-36 g L^{-1}) beneath one or more layers of limnetic to polyhaline water (Yager *et al.* 1994). Below the density interface, such ecosystems support a wide range of relict life forms that comprise a community whose general structure is predictable from the Caribbean region, the Canary Islands and north-western Australia (*e.g.* Baltanas & Danielopol 1995; Yager 1981, 1987a,b, 1989, 1994; Yager & Schram 1986; Holsinger 1989; Danielopol 1990; Yager *et al.* 1994; Yager & Humphreys 1996; Danielopol *et al.* in press).

Remipedes have always been collected beneath a density interface (thermo-halocline) in hypoxic water of 0.1-0.22 mg L^{-1} DO, sometimes beneath a layer of hydrogen sulphide (Yager 1994; Yager *et al.* 1994). The integrity of such anchialine ecosystems may depend on the maintenance of this stratification. Filamentous sulphur bacteria of the *Beggiatoa-Thiothrix* group can be common in anchialine caves and their hypothesised contribution to primary production by chemoautotrophy (Yager 1991a; Yager & Humphreys 1996) has been supported using stable isotope analyses (SIA: Pohlman *et al.* 1997).

The only deep anchialine system known in Australia, and the only continental anchialine system known in the southern hemisphere (see Iliffe in press: Fig 1), is Bundera Sinkhole in north-western Australia. This ecosystem includes the only known site for the crustacean class Remipedia in the southern hemisphere (Yager & Humphreys 1996), in an area containing the characteristic higher taxa of stygobiont crustaceans comprising thermosbaenaceans, hadziid amphipods, ostracods, cirolanid isopods, mysids, and caridean shrimp (Humphreys in press). In this arid area the surface layers are not fresh but have a salinity about half seawater rising to seawater at depth (Yager & Humphreys 1996).

This study documents the gross physico-chemical profile of the Bundera Sinkhole (temperature, salinity, dissolved oxygen, pH, redox), and the fine scale distribution at selected depths of H_2S and dissolved

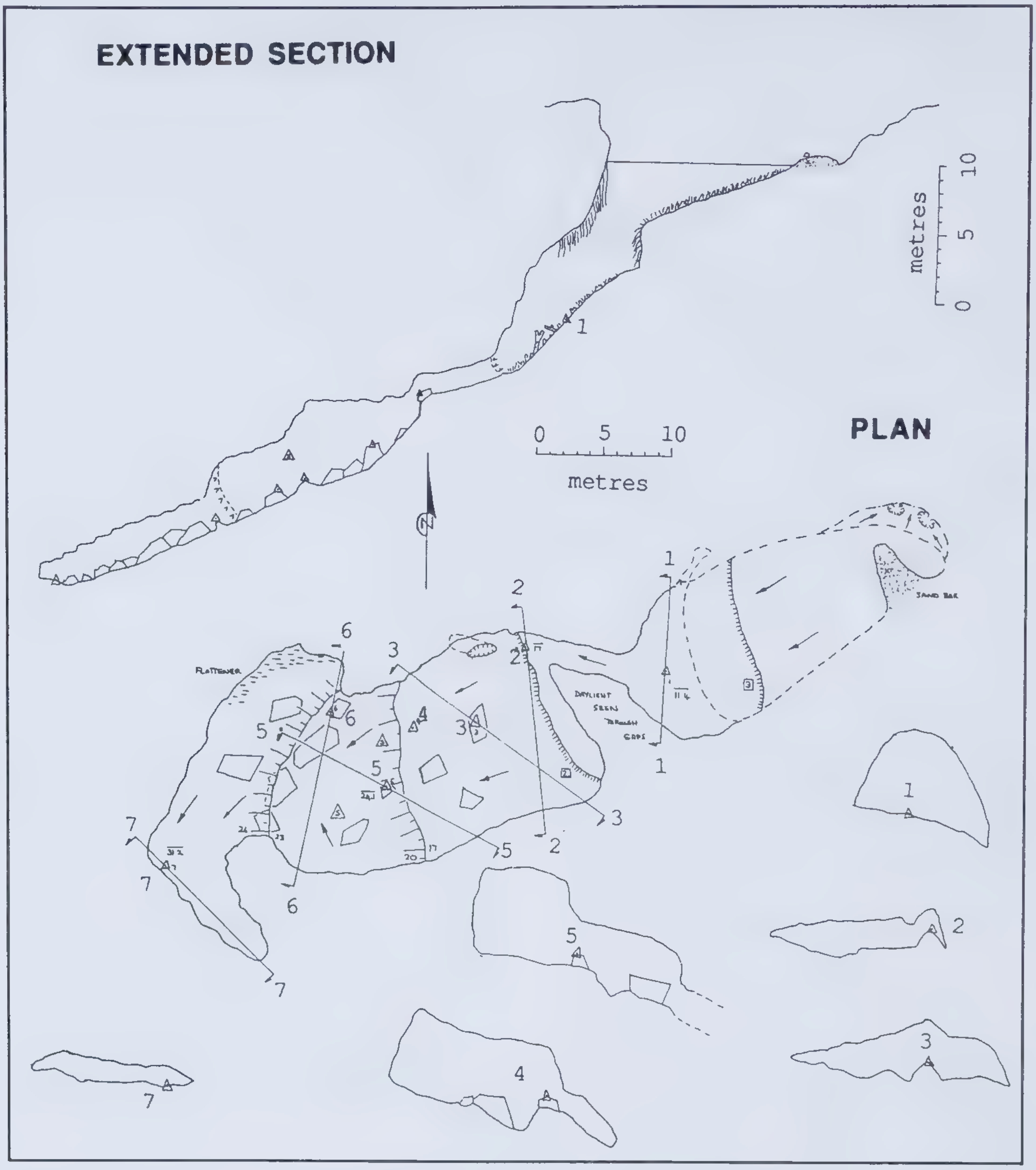

Figure 1. Plan and extended section of Bundera Sinkhole. The floor is mainly boulder breakdown. Algal/bacterial growth is depicted by the fringes near the top of the section. The lines vvvv denote the limit of ambient daylight and the limits of daylight sighting under optimal (first-dive) conditions. The numbered lines in the plan denote the location of the cross sections below numbered 1 to 7. Surveyed by A Poole and D Warren, 24-26 May 1995 to Grade BCRA Standard 3C.

inorganic nitrogen species (nitrite, nitrate and ammonium), and the stable isotope signatures ($\partial^{13}C$ and $\partial^{15}N$) of various components.

Methods

Bundera Sinkhole

The flooded sinkhole is located on the Cape Range peninsula in north-western Australia and is situated 1.7 km inland from the Indian Ocean. The cave has a single entrance from which a flooded passage, inclined at *ca.* 30° from the horizontal, extends about 70 m (Fig 1) to a maximum depth penetrated by divers of 33 m. The sinkhole is situated in the middle of a flat, 4.5 km wide coastal plain and the water table lies *ca.* 5 m below the surrounding surface. The depth to water and the small area of the sinkhole (*ca.* 10 x 20 m) will contribute to the stability of the water profile by shielding it from the often strong winds.

Characteristic of anchialine systems, the water level is influenced by the semi-diurnal marine tides of the area and which have an amplitude *ca.* 16% of the ocean tides (Humphreys *et al.* 1999). The tidal influence also affects the sinkhole in other ways; at high water the algal mats are submerged and the water surface is clear, but at low water the algae are emergent and, by spreading over the surface, greatly restrict light penetration.

A number of obligate subterranean species occur in the sinkhole below the thermo-halocline and are known only from this site. They include *Lasionectes exleyi* Yager & Humphreys (Remipedia), *Danielopolina* sp nov Danielopol *et al.* in press (Ostracoda: Halocyprida:

Thaumatocyprididae), *Liagoceradocus branchialis* Bradbury & Williams (Crustacea: Hadziidae), as well as the more widespread species *Stygiocaris stylifera* Holthuis (Decapoda: Natantia: Atyidae) and *Milyeringa veritas* Whitely (Perciformes: Eleotridae). Above the thermo-halocline are found the algae *Rhizoclonium ?tortuosum* (Dillw) Kuetz (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr) J Gr (Charophyta: Characeae), and the invertebrates ?Spionidae (Annelida: Polychaeta), *Halicyclops* sp nov (Copepoda: Cyclopidae), *Phlyctenophora* sp Brady (Ostracoda: Cypridacea), *Iravadia* sp (Mollusca: Iravadiidae), water striders *Limnogonus* (L) *fossarum gilguy* Andersen & Weir (Gerridae: Hemiptera) and *Kiefferulus intertinctus* Skuse (Chironomidae, Diptera).

Climate

The climate of the Cape Range peninsula is hot (mean daily temperature of *ca.* 27 °C) and arid and the annual evaporation (3219 mm) greatly exceeds the sparse precipitation (median 280 mm). Vegetation in the immediate vicinity of the sinkhole comprises predominantly hummock grassland and occasional shrubs.

Diving

The cave is thought to have been dived on only six sessions covering the years 1991 to 1998. Diving has mostly been conducted using SCUBA gear typical of that used for cave diving with built in redundancy. The current samples were collected using rebreathing gear (Dräger Atlantis) to minimise the impact of diving on the water column (Humphreys *et al.* 1999), known to be highly stratified (Yager & Humphreys 1996; WF Humphreys unpubl. obs.).

Sonde

Vertical profiles of depth (m), temperature (°C), dissolved oxygen (DO, mg L^{-1}), redox (mV), pH, and salinity (mg L^{-1} TDS) were made using a 44 mm diameter sonde (Datasonde3 Multiparameter Water Quality Datalogger DS3, Hydrolab Corporation, Austin, Texas) in untethered mode. During the first dive the sonde was pushed (sensors foremost) by the lead diver to record the undisturbed water column and sampling every second. The probes were calibrated against appropriate standards traceable to international standards. A LoFlow membrane was used on the DO probe without a stirrer. DO readings were calibrated to a salinity (TDS) of 18 g L^{-1} and not further corrected. Redox values were measured with a silver-silver chloride reference electrode and the readings offset to be based on the standard hydrogen electrode using the European convention (reducing environment negative). The data were transferred to a computer at the end of the dive.

Sample collection

Debris, sediments, animals and plants were collected from the immediate environment and at various depth in the sinkhole. Divers collected fauna and organic detritus from the sinkhole using towed plankton nets and hand-held suction devices, nets and bottles. Sediment and organic samples were collected into vials or polyethylene bags for transport to the surface. Terrestrial vegetation samples were stored in polyethylene bags. Organic samples for SIA analysis were frozen until dried in an oven at 45 °C and ground under liquid nitrogen. Chemical analysis was conducted on water samples collected through a range of depths determined from the redox and DO profiles measured during the first dive. The water samples were collected using a 50 mL syringe at predetermined depths measured with a gauge.

Chemical analyses

Total acid soluble sulphides (as mg L^{-1} S; referred to as H_2S in the text) were determined on site using a Chemetrics test kit (CHEMets sulphide R-9510, range 0-1 and 1-10 ppm). Nitrite, nitrate and ammonium nitrogen were determined within seven days by an analytical laboratory (Chemistry Centre, Perth) of samples frozen in the field. The standard methods used (Anon 1995) were; nitrogen, ammonium fraction 4500-NH_4^+ G automated phenate method; nitrogen, nitrite fraction, 4500-NO_2^{2-} B colorometric method; nitrogen, nitrite + nitrate fraction, 4500-NO_3^- F automated cadmium reduction method. Throughout square parentheses are used to denote concentration *e.g.* [H_2S] is hydrogen sulphide concentration.

Stable isotope analysis

Organismal metabolism utilizes the isotopes of an element differentially. Such 'fractionation' of the isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) occurs in predictable ways such that consumers are typically enriched (are 'heavier') by about 3-5 ‰ in ^{15}N and 1-2 ‰ in ^{13}C relative to their food source (Ehleringer *et al.* 1986). Hence, stable isotope analysis (SIA) of nitrogen and carbon is a powerful tool to examine food webs (Peterson & Fry 1987; Lajtha & Michener 1994) and technical advances have recently allowed it to become a routine method in ecosystem and other studies.

Ecological studies express the isotopic composition in terms of ∂ values which are the parts per thousand differences from a standard:

$$\partial X = [(R_{sample}/R_{standard}) - 1] \times 10^3,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ and the standards respectively are the Pee Dee Belemnite and nitrogen gas in the atmosphere (Peterson & Fry 1987).

SIA was conducted on plants and animals sampled both above the thermo-halocline (mollusc *Iravadia* sp, blind cave fish *Milyeringa*, girrids and tubificid worm, and in the deep cave below the thermo-halocline and layers of hydrogen sulphide (atyid shrimp *Stygiocaris*, *Milyeringa*) and the algae *Rhizoclonium ?tortuosum* (Dillw) Kuetz (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr) J Gr (Charophyta: Characeae). In addition, plants sampled from the immediate area included *Acacia* phyllodes and the hummock grass, *Triodia pungens*.

Total carbon and nitrogen and the fractionation of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ determinations were made by the stable isotope facility, Centre for Catchment and In-Stream Research, Griffith University, Queensland, using an automated Dumas combustion elemental analyser ('Roboprep', Europa Scientific, Crewe, UK) interfaced directly with a triple collector mass spectrometer ('Tracermass', Europa Scientific). The precision of the mass spectrometer, derived from the standard deviation of results of a replicated series of standards within a given sample run, are 0.5 delta units for nitrogen and 0.3 delta units for carbon (pers. comm., M Sutton, Griffith University).

Results and Discussion

Here the physicochemical profile of the water in the sinkhole is described together with aspects of the associated microbiological community. The low oxygen levels and the stable isotope signatures of the biota are discussed as to the evidence they provide supporting chemoautotrophic energy fixation in the sinkhole. Finally the characteristics of Bundera Sinkhole are considered in relation to comparable systems elsewhere.

Physico-chemical profile

The water column exhibited strong physico-chemical stratification with the different parameters exhibiting different types of stratification.

Temperature and salinity. There was a sharp thermocline at *ca.* 7.5 m where the temperature increased from about 21.0 to 26.5 °C, remaining close to this temperature to the depth of the cave (Fig 2A). The upper part of the profile can be in direct sunlight as it lies within the open part of the sinkhole (Fig 1). Under conditions of optimal visibility ambient day light penetrates to a depth of *ca.* 15 m and the entrance can be seen from a depth of *ca.* 25 m (Fig 1).

Surface salinity was *ca.* 19 g L^{-1} down to a marked halocline at 7.5 m (Fig 2A). below which the salinity increased to *ca.* 24 g L^{-1} and from which level salinity increased steadily to 32 g L^{-1} at a depth of 15 m. The salinity then remain relatively constant increasing to 34 g L^{-1} at a depth of 33 m (local seawater is 36.5 g L^{-1}).

As expected, the deep temperature of *ca.* 26 °C is close to the mean annual surface temperature of the area (*ca.* 27 °C on the east coast) and it appears stable between years (Humphreys *et al.* 1999). The substantially cooler surface water probably results from evaporation from the exposed surface into the dry atmosphere. While thermal

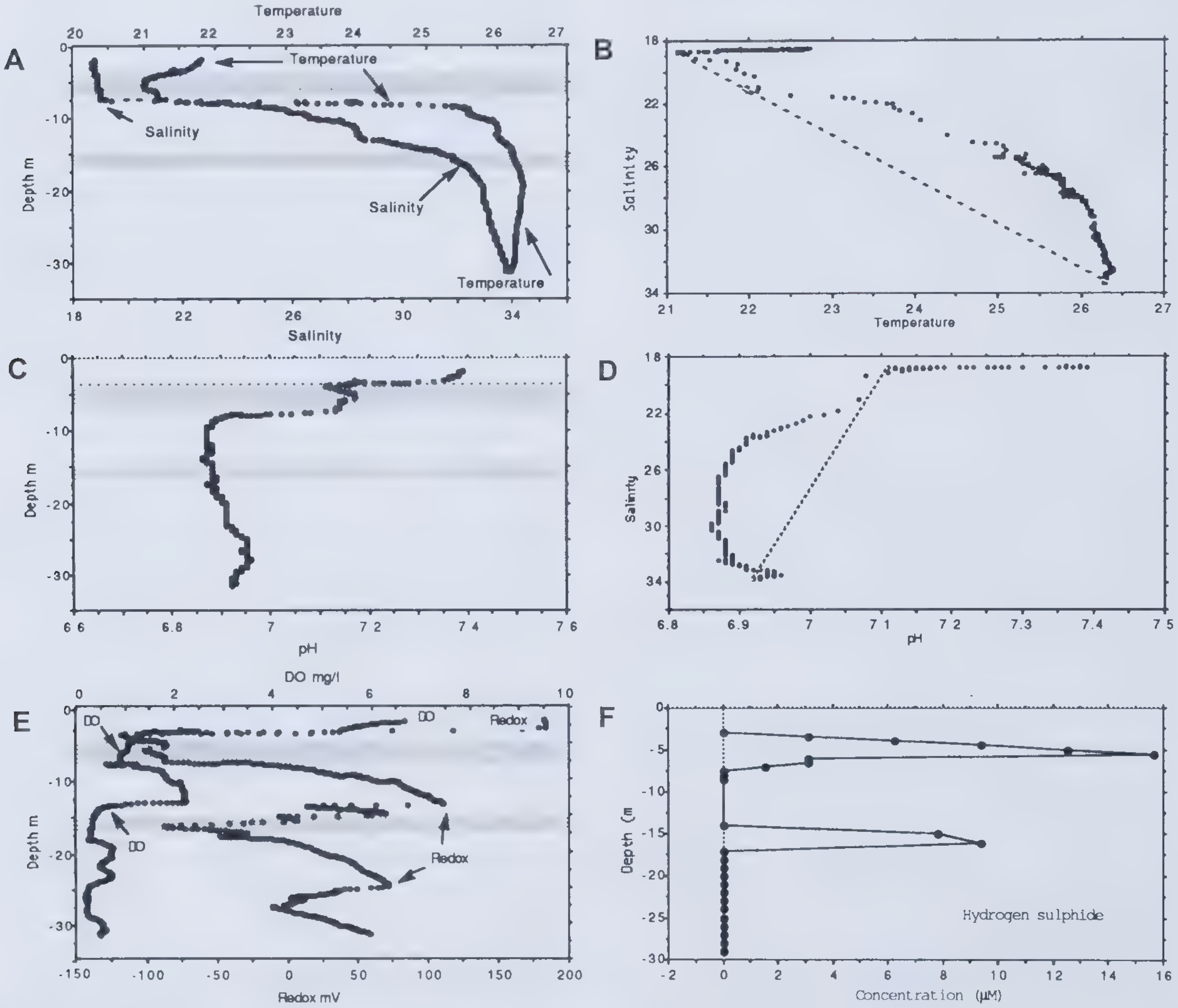

Figure 2. Profiles of Bundera Sinkhole in 1997 where the grey bands denote the zones of elevated hydrogen sulphide concentration (see Fig 3F), the descent rate was 0.05 m s^{-1} (sd 0.028, n=21). **A**; Temperature (° C) and salinity (g L^{-1} TDS) profiles. **B**; the salinity-temperature relationship of the vertical profiles where the dotted line denotes the conservative mixing hypothesis. **C**; pH profile. **D**; the salinity-pH relationship of the vertical profiles where the dotted line denotes the conservative mixing hypothesis. **E**; dissolved oxygen (mg L^{-1} DO) and oxidation reduction (redox) potential (mV) profiles. **F**; the vertical distribution of H_2S (as total acid soluble sulphides, µM).

exchange with the surface is continuous, the sparse freshwater input at the surface is spasmodic and unpredictable (Humphreys *et al.* 1989) hence there is ample time for a broad zone of mixing (Fig 2A) to develop between the lower sea water and upper brackish water increasing in salinity with time owing to evaporation from the surface. The non-conservative mixing (Fig 2B) between temperature and salinity indicates that the water had warmed since entering the ground-water.

Temperature and salinity, the parameters most commonly measured to examine the physico-chemical profiles of water, had a fairly simple profile with an inverted thermocline but the salinity and temperature profiles were not concordant, with the halocline being much broader than the thermocline (Fig 2A). However, together these parameters provide a markedly oversimplified picture of the complexity of the vertical stratification present in Bundera Sinkhole.

Hydrogen ion concentration. pH declined from greater than 7.5 at the surface to *ca.* 6.9 at *ca.* 8 m at the bottom of the thermocline and then remains between *ca.* 6.9-7.0 to the bottom of the water column (Fig 2C). Below the thermo-halocline the pH was fairly constant (6.90-6.96; Fig 2D). Non-conservative mixing is revealed by plotting pH against salinity (Fig 5) and due to hydrogen ion production at the halocline. This pattern is similar to that reported for the Mayan Blue Cave system, Mexico (Pohlman *et al.* 1997), but the details are different possibly due to the high photosynthetic activity in the surface waters of the sinkhole.

Dissolved oxygen and redox. DO fell rapidly from supersaturated at the surface to a minimum at about 7.5 m depth followed by additional minima at *ca.* 17 m and 27 m depth (Fig 2E). The complex DO curve is associated with the zones of increased [H_2S] although they are not entirely concordant. Stratification in the redox potential (Eh) was markedly polyphasic ranging from -125 mV to +175 mV. The redox minima correlated with oxygen minima but did not exactly map them; while each oxygen minimum occurred through a broad depth range (*ca.* 5 m), a redox minimum occupied only a narrow depth range in depth (Fig 2E).

Hydrogen sulphide. Two layers of elevated hydrogen sulphide, also detected by divers, were recorded at *ca.* 5 m and 16 m (Fig 2F) loosely concordant with the upper two

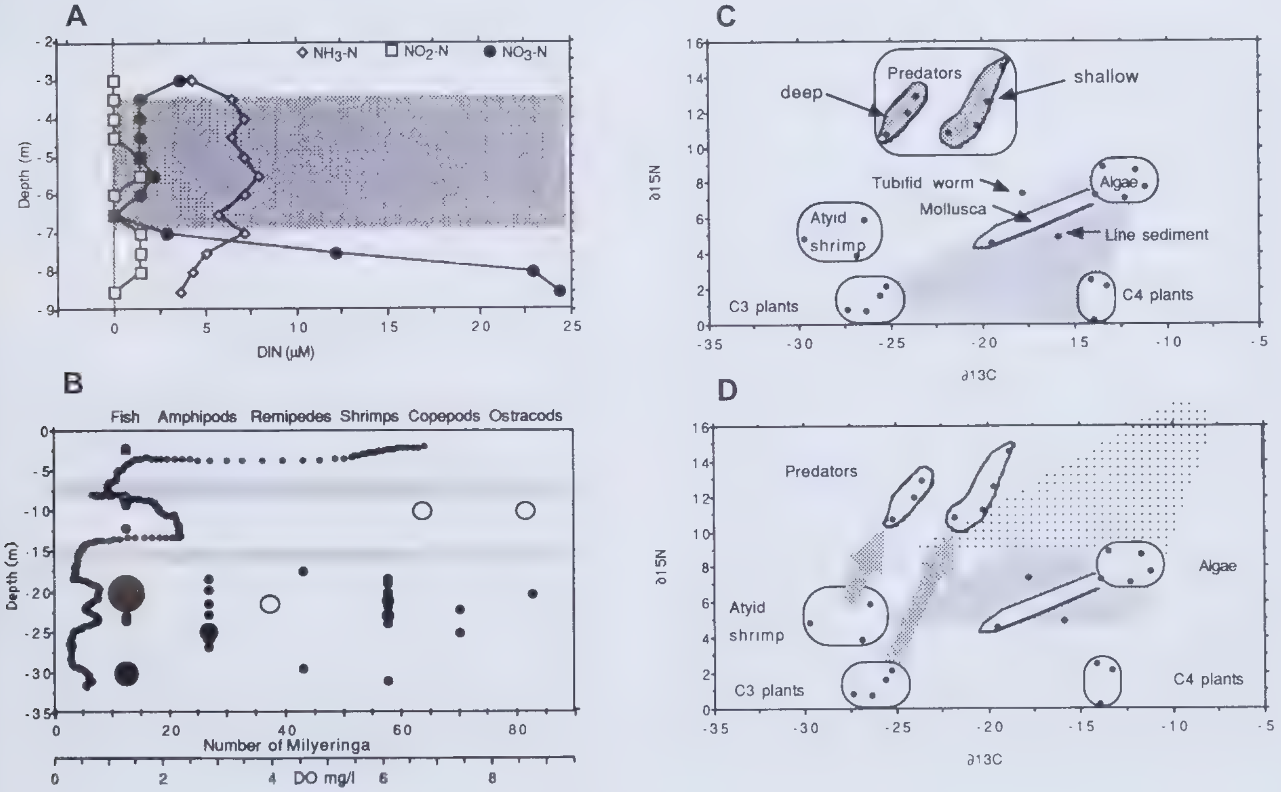

Figure 3. A; Vertical profile with depth of the dissolved inorganic nitrogen species (DIN µM) N-NH_4, N-NO_2, N-NO_3, shading denotes the region of elevated H_2S concentration (see Fig 2F). **B;** vertical distribution of sightings of the fauna in Bundera Sinkhole reported by divers, a) the closed circles denote the vertical distribution of the taxon named at the head of the column, b) the open circles denote the number of blind gudgeons (*Milyeringa veritas*) counted at one occasion at each of three depths (second bottom scale), c) the curve denotes the DO concentration (bottom scale), d) the grey bands denote the zones of elevated hydrogen sulphide concentration (see figure 9). These data are illustrative only as no regular sampling has been conducted through time. **C;** scatter plot of ^{13}C ‰ and ^{15}N ‰ values for samples from Bundera Sinkhole. If the food source is hypothesised to be some mix of C_3 and C_4 plants and algae then the average ^{13}C and ^{15}N values would lie in the polygon linking these data (shaded area). Data for plants with C_3 and C_4 metabolism, and algae are outlined, as are predators (left group, deep cave *Milyeringa*; right group, shallow cave *Milyeringa* [x3], gerrid [x1]), molluscs and worms. **D;** scatter plot of ^{13}C ‰ and ^{15}N ‰ values for samples from Bundera Sinkhole. If the food source is hypothesised to be some mix of C_3 and C_4 plants and algae then the average ^{13}C and ^{15}N values would lie in the polygon linking these data. This is represented as a shaded area but it has been displaced by one (heavy shading) and two (light shading) trophic increments of respectively 2 ‰ for ^{13}C and 4 ‰ for ^{15}N.

DO and redox minima (Figs 2F, 3A). Owing to the sampling resolution at depth in the sinkhole an additional layer of elevated H_2S associated with the deepest redox minimum may have been missed. In sediments, also, there can be a similar close correlation between the redox and S^{2-}-ion activity (Fenchel & Finlay 1995:11). This result at Bundera contrasts with the finding of Pohlman *et al.* (1997, in press) who recorded no dissolved sulphides (<2 µM) in the water column of an anchialine cave.

The maximum recorded H_2S was 15.6 µM. This compares with 250 µM H_2S in freshwater of Movile cave (Sarbu in press; Table 1), the most notable sulphide driven subterranean ecosystem, but other chemoautotrophic sulphide caves systems are being recognized (Sarbu *et al.* in press; Pain 1998).

Dissolved inorganic nitrogen species. Large changes in the vertical distribution of the DIN species are associated with the thermocline (Fig 3A). $N\text{-}NH_3$ is elevated in the upper H_2S layer that lay on the thermocline, while $N\text{-}NO_3$ increases markedly at the thermocline. It is not known whether a similar stratification of the DIN species occurs associated with the deeper hydrogen sulphide layer (Fig 2F), or the even deeper redox minimum (Fig 2E). The upper layer of hydrogen sulphide in the sinkhole is directly related with the changes in $[N\text{-}NH_3]$ ($Fs_{1,10}$ = 10.56, P = 0.009), an association previously unreported for an anchialine system.

The greatest $[N\text{-}NO_3]$ recorded was 24 µM, similar in magnitude to that found by Pohlman *et al.* (1997, in press), but the concentration was still increasing with depth at the lowest sample. However, data from 1994 (Yager & Humphreys 1996) suggest that it will decline to *ca.* 4 µM at a depth of 14 m (similar levels of $N\text{-}NO_3$ were recorded at 6 m in 1994 and 1997, respectively 1.07 and 1.43 µM). The $[N\text{-}NH_3]$ is inversely related to the $[N\text{-}NO_3]$ ($Fs_{1,10}$ = 14.82, P = 0.003). These data are consistent with nitrification (Ward 1986), a chemoautotrophic process when ammonium (NH_4^+) is successively oxidised to nitrite (NO_2^{2-}) and nitrate (NO_3^-), an exclusively aerobic process that takes place in the oxic-anoxic boundary layer (Fenchel & Finlay 1995:219). Similar data have been recorded in an anchialine system in Quintana Roo, Mexico (Pohlman *et al.* 1997, in press:11).

An inverse linear relationship between nitrate concentration and salinity was found in an anchialine system by Iliffe *et al.* (1984) and this generally implies conservative mixing and a single freshwater source (Burton & Liss 1975). The opposite relationship between $N\text{-}NO_3$ and salinity was recorded in Bundera Sinkhole ($Fs_{1,10}$ = 112.1, P < 0.001). As the concentration of $N\text{-}NO_3$ in seawater is less than in the sinkhole (data in Yager & Humphreys 1996: Table 1) then the increased concentration of $N\text{-}NO_3$ from 6 m to 14 m depth suggests that NO_3 is accumulating in the anchialine system. This finding implies that nitrogen fixation is occurring in the anchialine system and is consistent with the data in Fig 3A) and with the findings of Pohlman *et al.* (1997, in press:11).

Microbiotic environment

Much of the surface of Bundera Sinkhole was covered by algal mats at low tide, but at high water these became submerged and the water appeared clear. So, light penetration into the cave will vary both diurnally and with a superimposed lunar periodicity. In the water column immediately above the thermocline are globular veils characteristic of *Thiovulum* bacteria, but not identified, and which typically enclose regions of elevated sulphide concentration (Fenchel & Finlay 1995). On the sediments are motile filaments (characteristic of *Beggiatoa* spp), which occur mainly in sediments, and therewere attached filaments which occur as 'aufwuchs' on solid surfaces (commonly T*hiotrix* spp).

White filamentous bacteria were photographed moving out of sediments, collected from around the thermocline in Bundera Sinkhole, up the walls of the collecting vessels, presumably tracking the vertical position of the oxygen-sulphide boundary (Fenchel & Finlay 1995:188). Observations on the bacteria samples from Bundera Sinkhole (PD Franzmann, Centre for Ground-water Studies, Wembley; pers. comm.) showed that in samples of globular bodies in the near surface waters there were some short rods, and a number of dinoflagellates (*Gymnodinium*-like) but no filamentous bacteria. At a depth of 8.3 m (at the upper oxygen minimum and where the redox value again just becomes positive) wall samples contained many unsheathed bacteria. There were also many filamentous bacteria (*Sphaerotilus*-like: Clamydobacteriales; *Beggiatoa*-like: Beggiatoaceae and some sulphur crystals) including many large segmented filaments (*Thioploca chileae*-like: Beggiatoaceae), and some eukaryote cysts and diatoms. At a depth of 10.4 m (near the second oxygen maximum) there were limited numbers of rod bacteria, large segmented filaments (*Thioploca chileae*-like >10 µm in diameter), and some larger eukaryote cysts. At a depth of 30.1 m (at the lower oxygen maximum) there were many sheathed bacteria, *Sphaerotilus*-like (some with Fe-III on sheaths), and many rods and some spore-formers. *Sphaerotilus* spp are able to deposit iron on the sheath but sulphur is not deposited in the cells. However, they are considered to be chemo-organotrophic, not lithotrophic, organisms utilizing readily biodegradable substrates.

Beggiatoa, the sister taxon to *Thioploca* (Teske *et al.* 1995), and *Thiothrix* (which was not identified in these samples) are large white gliding filamentous sulphur oxidizing bacteria (chemolithoautotrophs) that may form mats in some anchialine systems as well as at deep sea hydrothermal vents and cold seeps. *Beggiatoa* are profuse in areas that are high in sulphide and combined nitrogen but low in dissolved oxygen (Ahmad *et al.* 1999) and their presence can be an indication of advanced eutrophication (Rosenberg & Diaz 1993). They are mixotrophic and some strains harvest sulphide oxidizing it to sulphate using oxygen as the electron acceptor (Hagen & Nelson 1997) but, as high concentrations of nitrate may occur in the vacuole (McHatton *et al.* 1996), it has been suggested that the oxidation of hydrogen sulphide, or endogenous stores of elemental sulphur, are used for the respiratory conversion of nitrate to ammonia.

Thioploca (and the recently described giant bacterium *Thiomargarita namibiensis*; Schulz *et al.* 1999) are common on continental shelves (Huettel *et al.* 1996) and belong in a small class of bacteria known to link the sulphur and nitrogen cycles. *Thioploca* spp and *Beggiatoa* spp inhabit aquatic environments at the oxygen-sulphide transition and where the negative chemotactic reactions to oxygen and sulphide are thought to keep both *Beggiatoa* and *Thioploca* at the optimal position for growth (Huettel *at al.* 1996).

There is a similarity between the upper 8 m of the profile in Bundera Sinkhole and that found at a microscale (4 cm) in marine sediments. In the sediments nitrate is continually replenished in the oxic zone by nitrifying organisms oxidizing the outward (up and down) diffusion of ammonia from the centre of the anoxic (H_2S) zone. In the dark, sulphide, thiosulphate and elemental sulphur are oxidized primarily by chemoautotrophic sulphur bacteria, most of which store sulphur and they therefore appear white in reflected light, hence the term 'white sulphur' bacteria. Most inhabitants of the microbial mat are motile and the chemolithotrophic sulphide oxidisers, such as *Beggiatoa* and *Thiovulum*, track the vertical position of the oxygen-sulphide boundary during changes in light intensity and they may even leave the sediment to form a white haze in the water, showing that the anoxic zone has rise above the sediment surface (Fenchel & Finlay 1995:186). If the anoxic zone reaches the photic zone then a characteristic purple sulphur bacteria is found immediately below the oxycline grading to a black sulphidic sediment. This general sequence of white motile colonies, through purple to black occurs associated with the oxycline in Bundera Sinkhole. In addition to areas of white sulphur bacteria in Bundera Sinkhole, were purple bacteria as typically found immediately below the oxycline if the anoxic zone reaches the photic zone (Fenchel & Finlay 1995). Below these areas were black sulphidic sediments on which the blind gudgeon *Milyeringa* were observed.

Concentrations of bacteria have also been reported from Cenote Angelita in Mexico, an anchialine sinkhole that, like Bundera Sinkhole, lacks significant water circulation. Degradation of organic matter, falling from the forest above, led to the production of H_2S that was utilized by the bacteria floating above the layer of 250 mM H_2S at the halocline (Pohlman *et al.* in press).

Anaerobiosis and biotic effects

Sulphide is very soluble in water and its dissociation characteristics are such that, at the pH values typical for natural waters, most of it is in the form HS^-. Since the gaseous form enters cells more easily that the ionized forms, the toxicity increases with decreasing pH. As it binds to cytochrome c oxidase and acts as a respiratory inhibitor, sulphide is extremely toxic to aerobic organisms and exposure to even micromolar concentrations is lethal for species lacking detoxification mechanisms (Fenchel & Finlay 1995:170).

Crustaceans are generally sensitive to anoxia and to sulphide and in sediments all crustaceans are confined to the oxic layers (Fenchel & Finlay 1995:167). Nonetheless, sulphide ecosystems (sulphureta) often contain populations of high density and surprising diversity in the vicinity of aerobic environments where nitrate and sulphate are regenerated from ammonia and sulphide through oxidation with O_2 (Fenchel & Finlay 1995:217). Epigean crustaceans may be extremely sensitive to both hypoxia and to the toxic effects of hydrogen sulphide (Hagerman & Vismann 1995). However, the fauna in Bundera Sinkhole apparently does not avoid areas where the DO is below 2.0 mL L^{-1}, and live below and between layers of high $[H_2S]$ (Fig 3B). The mechanisms by which the crustaceans and the fish survive these apparently inhospitable waters remains to be investigated.

Owing to the importance of low oxygen level in palaeoecology (Fischer & Arthur 1977; Kaiho 1991) and the biology of the water/substrate interface and of sediments (Fenchel & Riedl 1970), a terminology has been developed to describe anaerobic conditions which is dependent on both the discipline and the type of organisms involved (Tyson & Pearson 1991; Fenchel & Finlay 1995). The division criteria are ecological and physiological, chemical and practical, respectively the avoidance of animals of concentrations below 2.0 mL L^{-1} DO, nitrate reduction below 0.2 mL L^{-1} DO, and the limit of the accuracy of the Winkler method of 0.2 mL L^{-1} DO (Sket 1996).

Sket (1996) was uncertain whether the deoxygenated layers in anchialine caves were completely devoid of oxygen, or only very hypoxic, because of the problem of measuring oxygen precisely under these difficult conditions, a problem exacerbated by the presence of hydrogen sulphide. The water column in Bundera Sinkhole probably covers the full range of oxic conditions; supersaturated by photosynthesis near the surface, through dysoxic (2.0-0.2 mL l^{-1}), suboxic (0.2-0.0 mL L^{-1}) to anoxic (0.0 mL L^{-1}) conditions associated with the hydrogen sulphide layers.

It would appear that the anaerobiosis in Bundera Sinkhole is caused by mechanisms typical of those found to occur in the upper few centimetres of sediments or to other illuminated aquatic microbiotic communities that contain steep gradients of oxygen and sulphide, such as those associated with black band disease in corals (Richardson 1998). I hypothesise that in the upper photic part of the sinkhole, photosynthesis by the algae and cyanobacteria oxidizes the environment during the day and the organic material they produce is broken down by aerobic heterotrophs, restoring the redox balance. However, light intensity falls with depth and the temperature increases markedly at the thermocline resulting in both a reduction in oxygen production and an increase in reaction rate. Furthermore, this is associated with a local stability as oxygen transport will be reduced in the absence of convection across the thermo-halocline. Together, these result in local depletion of oxygen. As degradation by anaerobic microbes takes over, the metabolic end-products (*e.g.* sulphide, hydrogen) will render the surroundings chemically reducing. These changes are most likely to occur in places where there is a large import of dead organic material — the photic zone of Bundera Sinkhole is eutrophic producing large amount of organic matter — and protection from turbulent or advective transport of water, respectively by the sinkhole walls and the thermo-halocline. While this process is well supported by the data for the upper sulphide layer, the uniquely repeating and sulphidic (and roughly concordant redox and oxygen minima) layers in Bundera Sinkhole (Fig 2E) is poorly documented and less obvious in origin. Nonetheless, it would seem that the typical remipede crustacean community is only found below the second sulphide layer (Fig 3B), and which itself is not associated with a thermo-halocline (Fig 2A).

Stable isotope analysis

The data for the stable isotope enrichment of both carbon and nitrogen are given in Fig 3C. They are grouped according to C_3 and C_4 plant metabolism (*Acacia* and *Triodia* respectively), algae, shrimps (Atyidae), predators (the blind gudgeon, *Milyeringa veritas*, and gerrids [one pooled sample]). Analysis is shown of pooled samples of tubificid worms and the mollusc *Iravadia* sp that inhabit the algal layer. Finally, the 'line sediment' represents the accumulation of particulate organic matter settling over more than a year onto the guide line at depths of 17.5 m and 21 m.

The overt organic input is determined by the local vegetation which in this arid area is hummock grassland (C_4 plants) with few scrubs and annuals (C_3 plants) at the time of sampling. Hence, the vast majority (>90%) of local vegetation coverage comprises C_4 plants on the shallow sandplain overlying a marine terrace cut into limestone which deeply covers the cave (Fig 1). Given the scant and episodic rainfall in this region the downward percolation of organic matter through the sand and limestone overlying the cave is likely to be sparse. There are a few plants in the sinkhole of both C_3 and C_4 plants but the predominant vegetation is the thick algal community in the water of the sinkhole and which sometimes covers the surface and extends to several metres below the water level. It mainly comprises the algae *Rhizoclonium ?tortuosum* (Dillw) Kuetz (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr) J Gr (Charophyta: Characeae) and is thickly populated by the mollusc *Iravadia* sp. Large colonies of bacteria occur near the thermo-halocline both in the water column and on the walls and floor of the cave.

Carbon. The $\partial^{13}C$ values for the C_3 and C_4 plants are within normal limits which have median values respectively of -27 ‰ and -11 ‰ (Lajtha & Marshall 1994). While the values of $\partial^{13}C$ for algae in Bundera Sinkhole are heavy compared with most values in the literature, they are not outside recorded limits. Values of $\partial^{13}C$ in marine algae are between -19 to -24 ‰ and are affected by the uptake of dissolved inorganic carbon in planktonic photosynthesis (Peterson & Fry 1987). In fresh water values of $\partial^{13}C$ vary widely depending on the source of dissolved CO_2; where respiration inputs are strong, the $\partial^{13}C$ values for dissolved inorganic carbon may approach -20 ‰, with algae reaching -45 ‰ owing to fractionation during carbon uptake (Peterson & Fry 1987). In algal cultures $\partial^{13}C$ variations ranging from -29.7 ‰ to -5.5 ‰ have been reported (Falkowski 1991), with about one third of this variation attributed to changing concentrations of CO_2 but the very high values near -5 ‰ were attributed to the active uptake of inorganic carbon (Goericke *et al.* 1994), hence these values could be influenced by the carbonate chemistry of the karst system itself. Anchialine systems, such as Bundera Sinkhole, have attributes of both freshwater and marine systems (owing to the marked physico-chemical stratification of the system, these occur in the same location) but the relative influence of the marine system using, for example, the $\partial^{14}S$ distribution (Peterson & Fry 1987), has not been investigated.

Nitrogen. The values of $\partial^{15}N$ for the C_3 and C_4 plants are within normal bounds (Peterson & Fry 1987) but the $\partial^{15}N$ values for the algae are high, for unknown reasons. While the fractionation of nitrogen isotopes is rarely greater than 2 ‰ in natural systems, it is often large (10-20 ‰ for nitrate or ammonium uptake by aquatic algae and microbes (Macko & Ostrom 1994). Where nitrate is abundant, as in the surface water of Bundera Sinkhole (Yager & Humphreys 1996), fractionation during assimilation by phytoplankton may lead to a $\partial^{15}N$ sufficiently heavy (Peterson & Fry 1987) to reach the level found in Bundera Sinkhole. Study of the isotopic fractionation in the cascade of DIN species in the upper water profile of the cave would help resolve these uncertainties.

SIA and trajectories. The line sediment, the tubificid worms and molluscs lie within the envelope of an hypothesised source of carbon and nitrogen derived from a mix of C_3 and C_4 plant material and algae (see Figs 3C, 3D). The predators form two groups depending whether they originate from superficial parts of the cave or the deep zone, with the former being 'heavier'; the gerrid data are consistent with this pattern. The atyid shrimps lie outside the hypothesised food mix envelope, being lighter. The trophic trajectories (Fig 3D) suggest that the two predator populations are derived from C_3 plants (two trophic steps removed), or atyid shrimps (one trophic step removed); *Milyeringa veritas* is known to eat the shrimps (Humphreys & Feinberg 1995).

As shown above, there is evidence from the stratification of the DIN species that nitrification was occurring in Bundera Sinkhole. Furthermore, visual observations in the main water body, observation of the characteristic motile behaviour of sulphur bacteria observed *in vitro*, and the presence of H_2S, suggest that sulphur bacteria are widely present at and below the thermo-halocline and these are likely to be involved in chemoautolithotrophy. Such chemosynthetic biomass is characteristically lighter (more negative $\partial^{13}C$) than photosynthetically derived carbon (Conway *et al.* 1994). While no isotope determinations were made on bacteria, these observations could be verified by stable isotope determinations of the bacteria.

One explanation for the lightness of the atyid shrimp data is that they are utilizing chemoautotrophic bacteria for part of their food source: atyid shrimp have a brush-shaped tuft of setae in the first two pereiopods with which they brush the substrate while feeding (Bailey-Brock & Brock 1993). Evidence in support of chemoautolithotrophy in anchialine ecosystems is presented by Pohlman *et al.* (1997 in press) for an anchialine cave in Mexico.

Comparison with other areas

The high surface salinity and the complexity of the profile in Bundera Sinkhole may be associated with the aridity of the area and hence minimal surface input and low ground-water flow of *ca.* 0.003 mm s^{-1} on the eastern side of the same peninsula. This results in a broad zone of diffusion, 20-30 m thick, between the overlying freshwater lens and the underlying seawater (Exmouth water supply borefield; Consultative Environmental Review; Water Corporation, unpublished, 1996). Bundera Sinkhole probably lies at the extreme seaward side of the system where only the diffusion zone is represented and thus exhibits only the brackish/seawater interface seen in the sinkhole.

Most anchialine systems that have been examined have a freshwater lens overlying sea water (Iliffe in press); the freshwater lens may be thick and increase in depth inland, for example, on the Yucatan Peninsula 2 km inland it is 10 m thick at sinkhole Abejas and 10 km inland it is 20 m thick at sinkhole Vaca Ha (Iliffe in press). At Wonderland Cave, Bermuda, brackish water overlies seawater, and this cave is most comparable to Bundera Sinkhole in its salinity profile (Iliffe in press: Fig 3).

A summary of published physico-chemical profiles of anchialine systems is given by Humphreys *et al.* (1999); Bundera Sinkhole is the deepest, and probably the smallest, of these. In Bundera Sinkhole there is a polymodal DO depth profile, a form shown in none of the published DO depth profile, all of which exhibit a unimodal DO depth profile. By inference it suggests that the other systems probably have a single H_2S layer should one be present.

The DIN species data for Bundera Sinkhole (Fig 3A) are very similar to those reported by Pohlman *et al.* (in press) in a cave where they obtained strong evidence, using stable isotope analysis, that chemoautotrophic energy fixation was occurring. This means that such systems, rather than being totally dependent on imported (allochthonous) energy sources, as is the general model for cave systems, they can derive part of their energy *in situ* from autochthonous energy fixation. This has considerable implications to anchialine systems because it means that energy may be available broadly through anchialine systems, even where the ground-water is covered by impermeable ceilings. In this context, it is worth noting that sulphide-oxidising mixotrophic *Thiothrix* and *Beggiatoa* bacteria, which may be primary producers using sulphide-based chemosynthesis (Brigmon *et al.* 1994; *cf.* Kane *et al.* 1994), occur widely in anchialine and other ground-waters (Yager 1991a; Brigmon *et al.* 1994), as well on deep-sea hydrothermal vents (Belkin & Jannasch 1989).

The physico-chemical environment in Bundera Sinkhole is very complex and this complexity is associated with biogeochemical processes that are likely to be of fundamental importance to the maintenance of the unique community contained in this anchialine cave. SCUBA diving alters the vertical stratification of the physico-chemical environment in the sinkhole (Humphreys *et al.* 1999) and the effects of this may be disruptive to the unique anchialine community inhabiting the cave. As some of the fauna associated with such anchialine systems have only ever been collected by divers, remipedes for example, then diver access is essential for biological work. However, this should be limited and where possible be conducted using rebreathing equipment. There is a lack of basic data on the gross physico-chemical environment in Bundera Sinkhole, on ground-water movement, temporal changes in the profile resulting from the effects of episodic rainfall on surface input as well as ground-water flow. A diver-free profiling system needs to be established to determine long term changes, particularly the establishment and maintenance of the complex redox profile, its associated chemolithotrophic organisms and the significance of these processes to the remipede community.

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Effects of research diving on the physico-chemical profile of Bundera Sinkhole, an anchialine remiped habitat at Cape Range, Western Australia

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Abstract

Bundera Sinkhole, in arid north-western Australia, contains a community of stygofauna, including remipedes and thaumatocypridid ostracods, its only known location in the eastern hemisphere. Water in the cave has a complex physico-chemical depth profile that is probably important to the functioning of this community. The effect of research diving on the physico-chemical profile was examined using, firstly, semi-closed circuit equipment (rebreathers) to minimise the physical and chemical disruption to the profile and, secondly, open circuit SCUBA to investigate the impacts of standard research diving operations. Both open and closed circuit diving had a measurable impact on the gross physico-chemical environment of the cave of blurring the interface between physico-chemical zones, but open circuit diving had a markedly more obvious impact. Importantly, diving extended the oxic zone downwards through a layer that previously contained a cascade of nitrogen species and a sulphidic layer in the vicinity of the thermo-halocline that is probably associated with chemoautotrophic production. The stratification in the redox environment was disrupted by both types of diving.

Introduction

Anchialine (or anchihaline) ecosystems are inland underground mixohaline waters affected by marine tides, usually with little if any surface exposure (Stock *et al.* 1986; Iliffe in press). Anchialine ecosystems often contain a diverse assemblage of relict species (Sket 1981, 1996); at least ten new families, and a new class (Remipedia) of crustaceans have been described from anchialine systems in recent years (GA Boxshall, Natural History Museum, London, pers. comm.).

Remipedes are typically found in communities consisting almost entirely of stygobiont crustaceans comprising thermosbaenaceans, hadziid amphipods, ostracods, cirolanid isopods, mysids, and caridean shrimp. While the general structure of these anchialine communities is predictable from the Caribbean region, the Canary Islands and north-western Australia (*e.g.* Baltanas & Danielopol 1995; Yager 1981, 1987a,b, 1989, 1994; Holsinger 1989; Danielopol 1990; Yager *et al.* 1994; Yager & Humphreys 1996), the detail of each is regionally unique at the mid to lower taxonomic levels.

Although these faunistically distinct and diverse ecosystems may have persisted though geological eras (Danielopol *et al.* in press; Humphreys in press a), they appear vulnerable to anthropogenic impacts and need to be the focus of conservation assessment to protect their relictual fauna, often endemic at higher taxonomic levels (class in the case of Remipedia). The reasons for the vulnerability of anchialine systems are several fold. The thin soil cover, typical of karst areas, provides little filtration of percolating fluids making them prone to ground-water contamination and the open conduit hydrological systems permit the rapid and distant spread of any introduced contaminants, be they nutrients or toxins. Furthermore, the flushing of groundwater will be exceptionally low in the arid Cape Range, and in the related anchialine ecosystems of Barrow Island (Humphreys in press b), making the residence time of contaminants long. The introduction of energy into subterranean systems changes the energy balance and the competitive abilities and permits epigean organisms to displace hypogean organism that are adapted to a low energy environment (Malard 1995). Hence, these ecosystems are sensitive to pollution (Iliffe *et al.* 1984; Notenboom *et al.* 1994), but paradoxically they may occur in widely variable and extreme physico-chemical conditions (Sket 1986; Humphreys 1999). Together these factors have led to anchialine systems becoming the subject of wide-spread conservation assessment (Sket 1981; Maciolek 1986; Brock *et al.* 1987; Ridgley & Chai 1990; Thomas *et al.* 1991, 1992; Iliffe 1992; Bailey-Brock & Brock 1993) and public interest (*vide* Waikoloa Anchialine Pond Preservation Area Trust Fund in Hawai'i; Brock *et al.* 1987). The red shrimps of the cosmopolitan family Atyidae, which contains many widely vicariant congeneric species (Holthuis 1986), that inhabit some anchialine pools are linked with mythology in some countries (*e.g.* Fiji, Hawaii and the Philippines) and social taboos have facilitated their conservation (Choy 1987).

Anchialine systems in drowned sinkholes (cenotes) are typically highly stratified, having a freshwater layer overlying and separated from warmer seawater by a marked thermohalocline or density interface (pycnocline; Yager & Humphreys 1996; Humphreys in press a). The characteristic anchialine fauna mostly inhabits this region of seawater (Yager & Humphreys 1996) which is typically hypoxic (Yager *et al.* 1994; Yager & Humphreys 1996), and may occur beneath one or more layers of hydrogen sulphide (Humphreys 1999). The pycnocline may also be associated with dense growths of sulphur and nitrifying chemoautotrophic bacteria (Pohlman *et al.* in press; Humphreys 1999). As all known remiped habitats exhibit such marked stratification, and as remipeds have only been collected by cave divers from beneath a density interface, the maintenance of this stratification may be required for the functioning of these anchialine ecosystems.

Bundera Sinkhole (numbered 6C-28 in the Australian Karst Index) is the only deep anchialine system known in Australia and is the only continental anchialine system known in the southern hemisphere (see Iliffe in press: Fig 1; Humphreys, 1999). This narrow cave is the only known site for the crustacean class Remipedia (*Lasionectes exleyi* Yager & Humphreys) in the southern hemisphere (Yager & Humphreys 1996) and the site lies outside conservation reserves. *Lasionectes exleyi* is listed as endangered under both Western Australian and Commonwealth of Australia legislation. In addition, Bundera Sinkhole is the only know locality for *Danielopolina* sp nov Danielopol *et al.* (Ostracoda: Halocyprida: Thaumatocyprididae), and is the only known eastern hemisphere location for that genus, and *Liagoceradocus branchialis* Bradbury & Williams (Crustacea: Hadziidae). A number of other stygal species are also found in the system; *Stygiocaris stylifera* Holthuis (Malacostraca: Decapoda: Natantia: Atyidae) and *Milyeringa veritas* Whitely (Perciformes: Eleotridae). The contiguous anchialine system also contains a number of other taxa with Tethyan disjunct distributions, including the genera *Haptolana* (Isopoda: Cirolanidae), *Halosbaena* (Thermosbaenacea), and *Ophisternon* (Pisces: Synbranchiformes), and gammarid amphipods (Humphreys 1993a,b,c; Barnard & Williams 1995; Bradbury & Williams 1996a,b, 1997a,b). Above the thermohalocline in the photic zone, this anchialine system also contains a number of non-stygal plants and animals; the algae *Rhizoclonium ?tortuosum* (Dillw) Kuetz (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr) J Gr (Charophyta: Characeae), and the invertebrates ?Spionidae (Annelida: Polychaeta), *Halicyclops* sp nov (Copepoda: Cyclopidae), ostracods, *Iravadia* sp (Mollusca: Iravadiidae), water striders (Gerridae: Hemiptera) and *Kiefferulus intertinctus* Skuse (Chironomidae, Diptera).

Diving is necessary to study these anchialine caves but the effect of diving, both research and recreational, needs to be assessed. Diving in these stable anchialine caves tends to disrupt the physico-chemical stratification by finning and rise of exhalent air from SCUBA equipment; these effects are enhanced in deep narrow caves by the confined escape route and progressive expansion of exhalent air. This disruption of the physico-chemical stratification is indicated by the reduction in visibility and by the loss of large bacterial colonies associated with the thermo-halocline. The disruption is likely to be more prolonged in systems where the flow of freshwater is limited by low recharge such as in arid northwestern Australia.

This study describes the geomorphological and hydrological context of Bundera Sinkhole, and documents the short-term effects of diving on the physico-chemical profile. We used rebreathing SCUBA to eliminate most of the bubbles from exhaust gases and thus reduce physical disturbance to the ecosystem and contamination through oxygenation or carboxylation. To examine disruption of stratification of the water column by open-circuit SCUBA, the final few dives in the sinkhole used open-circuit SCUBA gear or rebreathers set on open circuit. In addition, we examined the limited data that are available for the longer-term stability of the system.

Methods

Bundera Sinkhole

Bundera Sinkhole is located on the Cape Range peninsula in north-western Australia, 1.7 km inland from the Indian Ocean in the middle of a flat, 4.5 km wide coastal plain. The flooded sinkhole starts in the Bundera calcarenite (the type section) deposited on a wave-cut platform, the lower of a series cut into the Tulki Limestone of Miocene age in the Cape Range anticline (Wyrwoll *et al.* 1993). The water surface is little disturbed by wind as the water surface lies *ca.* 5 m below the lip of the sinkhole, the opening of which is quite small (*ca.* 10 x 20 m). The flooded sinkhole leads into a passage, inclined at *ca.* 30° from the horizontal, which extends about 70 m (Fig 1 of Humphreys, 1999) to a maximum depth penetrated by divers of 33 m. The main cave extends towards the west but there are minor easterly passages in line with a gorge entering the coastal plain 2.8 km to the east.

Characteristic of anchialine systems, the water level is influenced by marine tides of the area. Comparison of the predicted amplitude of coastal tides at Norwegian Bay (24 km south; Anon 1996) with the recorded tides from Bundera Sinkhole shows the amplitude in the sinkhole (0.61 ± sd 0.24 m, n=17) to be 16% ± sd 0.05% of the ocean amplitude (0.09 ± sd 0.04 m, n =17). The semi-diurnal form of the ocean tidal curve is reflected in the sinkhole (Fig 1A) but the range of the diurnal tide changes little over the lunar cycle and the general water level increases towards spring tides and decreases around neap tides (Fig 1B) giving an overall range of *ca.* 0.35 m. It is not evident if the thermo-halocline moves vertically with the tides. The tidal influence also affects the sinkhole in other ways; at high water the algal mats are submerged and the water surface is clear, but at low water the algal mats spread over much of the surface and greatly restrict light penetration.

Climate

The climate of the Cape Range peninsula is arid and annual evaporation (3219 mm) greatly exceeds the sparse precipitation (median 280 mm). Mean daily temperature is *ca.* 27 °C but the mean monthly maximum temperature

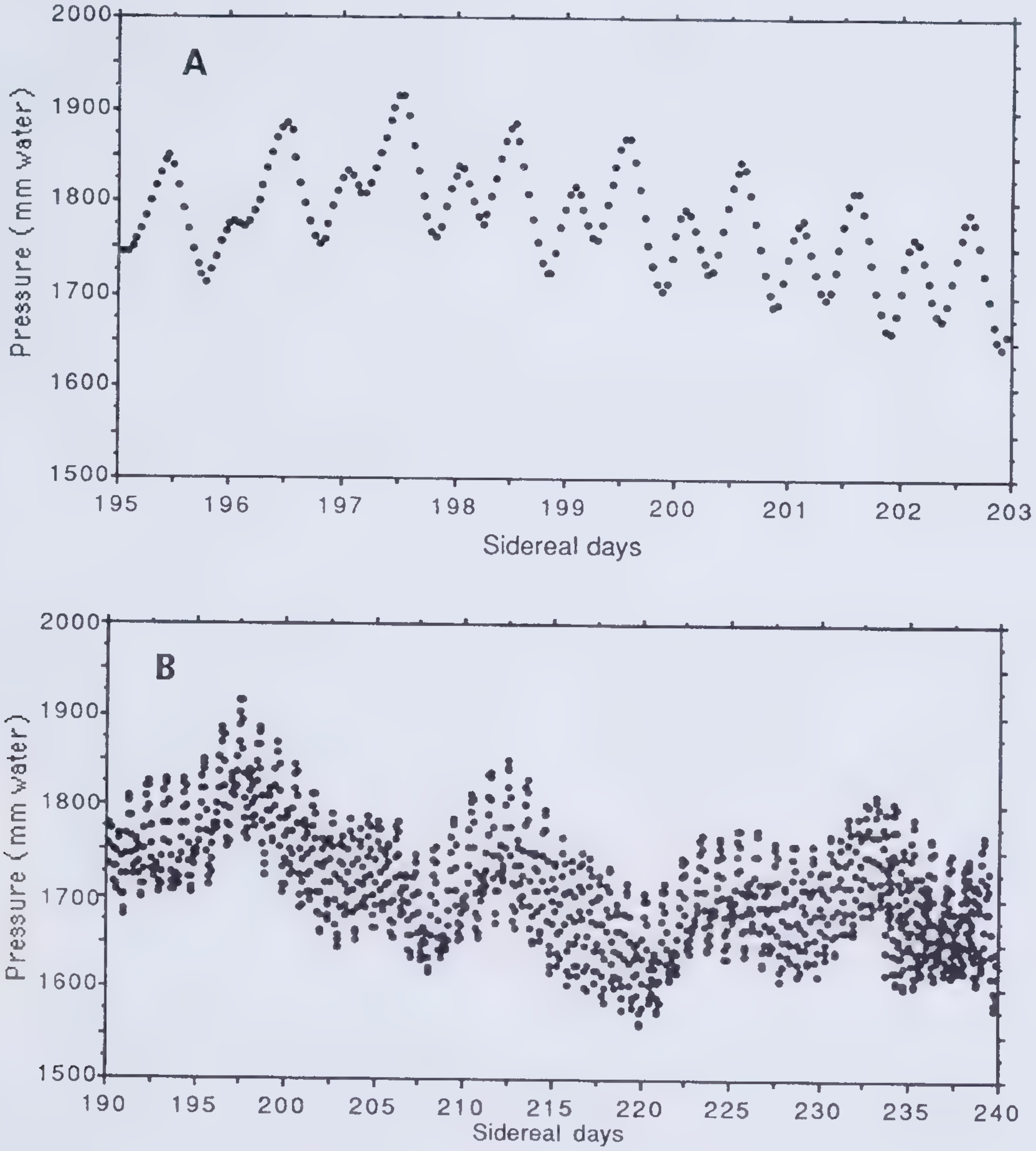

Figure 1. Tide recording in Bundera Sinkhole showing the semi-diurnal tides. **A**: 8 day period. **B**: 50 day period.

exceeds 35 °C for four months of the year. Relative humidity is low (mean at 9 am = 53%; at 3 pm = 33%) and the rainfall is sporadic, predominantly falling in large episodes of various meteorological origins (Beard 1975; Gentilli 1979). The infrequent large rainfall events flood the caves deeply, at mean intervals of 56 months (Humphreys *et al.* 1989), and are the major recharge episodes of the freshwater aquifers.

Regional ground-water

The general hydrogeological model for oceanic islands has been applied to the ground water of Cape Range peninsula (Allen 1993). Following the Ghyben-Herzberg principle, a fresh water lens overlies salt water so that locally a wedge of salt water intrudes under the fresh water contained in the limestone, and between which a zone of mixing occurs that broadens towards the coast. In the Exmouth area, on the north-eastern part of the Cape Range peninsula, the freshwater-seawater transition, at about five kilometres from the coast, is exceptionally far inland (Martin 1990). This considerable inland extent is related to the high transmissivity of limestone, low groundwater flow resulting from the aridity of the Cape Range area, and lowering of the water table through water abstraction (Davidson 1995). In the Exmouth area, the inland limit to the salt-water interface appears to be controlled by the presence of solution cavities and channels below the water table (Martin 1990). Comprehensive chemical analysis of the water above and below the thermohalocline in Bundera Sinkhole was given in Yager & Humphreys (1996).

Diving in Bundera Sinkhole

The first recorded dive in the sinkhole was in 1991 to a depth of three metres in the narrow eastern extension of the cave (R Cooper, Perth, pers. comm.). The cave was first penetrated fully on 6 August 1993, specifically to search for the remipedes that had been predicted to occur in the area (Poore & Humphreys 1991; Yager & Humphreys 1996). Research diving conducted from 6-12

August 1993, 19-21 March 1994, 24-26 May 1995, 21-24 September 1997 was partly reported by Yager & Humphreys (1996). We know of only two other dives on this site, by sports divers on a single occasion in 1998.

The diving gear employed was typical of that used for cave diving, with redundancy. The Dräger "Atlantis" rebreathers used in 1997 were modified to have the required redundancy. These are a semi-closed circuit design in which the exhalant air is passed through soda lime to remove carbon dioxide, and then recirculated. Only a small amount of gas escapes into the water during use, the amount depending on the flow rate which is preset by the diver to suit the diving depth and the work rate. The rebreathers were modified by the addition of bubble diffusers to minimise large, rapidly rising, bubbles. The gas release rate was reduced by fine adjustment to the initial gas introduction rate and the gas mix. This resulted in an almost negligible off-gassing at the operating depth, extended the bottom time, and reduced the overt disturbance of the water column.

In 1997, the total dive time was 16.7 hours comprising 17 person-dives in seven dive sessions, mostly to the full depth of the cave (33 m). Twelve person-dives totalling 11.8 hours were made using rebreather equipment, followed by five totalling 4.9 hours using either the rebreathers on open circuit or standard SCUBA gear.

On our first entry to the cave in 1993, and our first dive in 1997, the full extent of the cave was recorded using a video camera (Sony Hi8), and additional video recording was taken in 1995.

Sondes

In 1997, two 44 mm diameter sondes (Datasonde3 Multiparameter Water Quality Datalogger DS3, Hydrolab Corporation, Austin, Texas) were used singly or together in untethered mode to record each parameter every 1 to 5 seconds throughout each dive. On the first and last dives, a sonde was pushed (sensors foremost) by the lead diver to record the undisturbed water column. At other times, to enable other tasks to be performed by the divers, the sondes were strapped upside down to the diver's breathing equipment so that the sensors were at the front of the diver. The data were transferred to a computer at the end of each dive. The sondes were fitted with sensors to measure depth (m), temperature (°C), dissolved oxygen (DO, mg L^{-1}), redox (mV), pH, and salinity (mg L^{-1} TDS). The probes were calibrated against appropriate standards traceable to international standards. A LoFlow membrane was used on the DO probe without a stirrer. DO readings were calibrated to a salinity (TDS) of 18 g L^{-1} and not further corrected. Redox values were measured with a silver-silver chloride reference electrode and the readings offset to be based on the standard hydrogen electrode using the European convention (reducing environment negative).

Tidal data

The tidal cycle in the sinkhole was recorded using a datalogger fitted with a pressure transducer (Model 392 logger; Dataflow Systems, Noosaville, Queensland); the mean value of two readings was recorded every 30 minutes. Readings were taken in the sinkhole for four months in 1996.

Disruption of physico-chemical profiles

Several methods were used to detect changes to the water column brought about by diving: 1) observations of divers and from video records; 2) examination of the depth profiles of various physico-chemical parameters; and 3) statistical analysis of specific points in profiles. The latter included change in depth at which a given value of a parameter was reached, change in value of parameter at a given depth, and changes between open and closed circuit diving. The differences between open and closed circuit diving, morning and afternoon diving, and progressively over time, were analysed using Mann-Whitney U test, two factor ANOVA, and linear regression.

Depth is recorded below the water surface (bws), rather than from a fixed location in the cave, to allow for tidal movement of the thermo-halocline.

Results and Discussion

The marked thermo-halocline of Bundera Sinkhole was present in all three years for which profile data are available, but the details of the stratification seem to vary between years as does the physical appearance of the water. In 1993, distinct thermoclines were reported by divers at depths of 8 m and 13 m (about the levels of the hydrogen sulphide layers in 1997; Fig 2A) , but their magnitude is unknown. Wispy suspensions, probably bacterial colonies, were seen in the water column at a depth of about 14 m, just below the cave entrance restriction. In 1994, the suspensions were barely visible and they were not present in 1995 when a distinct tannic layer occurred at a depth of 22 m. A strong smell of hydrogen sulphide was encountered in all years in the vicinity of the density interface. In 1997, a marked refractive layer at about 8 m depth was observed at the start of the thermohalocline.

Surface water in the sinkhole is thick with algae and below which, on the initial dive in 1993, there was a zone of large insubstantial globular structures (probably bacterial monofilms) together with a zone of large chain-like filamentous structures (probably colonial sulphur bacteria) that are consistent in form with those ascribed to the *Beggiatoa-Thiothrix* group common in anchialine caves containing remipedes in the Caribbean region (Yager 1991). Similar structures ('sulphuretas') have been reported from otherwise afaunate caves in the Nullarbor, southern Australia (J James, Sydney University, pers. comm.). The massive bacterial colonies seen in mid-water on first entry in 1993 have not subsequently been seen to be as well developed. The reason is unknown, but could be the result of diving, rainfall or ground-water flow. However, filamentous and globular colonies of bacterial colonies were collected from the walls and floor of the cave in 1997.

Over a sequence of SCUBA dives in 1993, water below the thermo-halocline initially had high clarity but visibility decreased markedly over five dives until it was necessary to follow the guide-line to exit the cave. By contrast, in 1997 visibility remained high and the guide-line was not necessary to exit the cave despite considerably more diving activity with rebreathers. Some

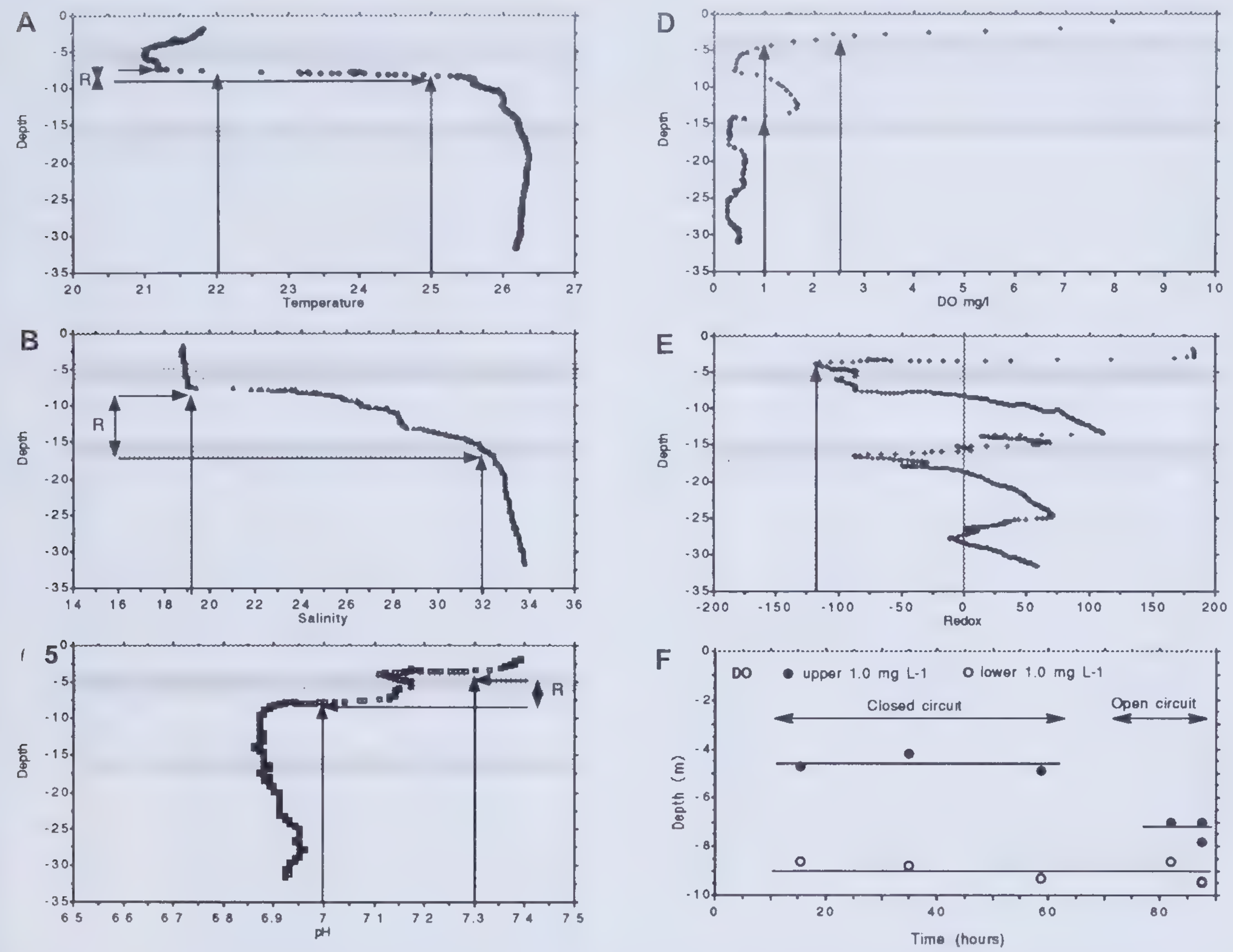

Figure 2. Vertical profiles with depth of various physico-chemical parameters in Bundera Sinkhole in 1997, statistical test were conducted on the values of the parameters shown by the single-headed arrows and the range of the parameters (R) shown by double-headed arrows: **A:** temperature (°C), where the grey bands denote the zones of elevated hydrogen sulphide concentration (see Humphreys 1999; Fig 2F). Descent rate was 0.05 m s^{-1} (sd 0.028, n=21). **B:** salinity (g L^{-1} TDS). **C:** pH. **D:** dissolved oxygen concentration (DO mg L^{-1}). **E:** oxidation reduction (redox) potential (mV). **F:** location (m below water surface) of the upper and lower DO minima in relation to the periods of closed and open circuit diving.

of this difference between 1993 and 1997 may have resulted from the earlier dislodgment of sediments by bubbling from open-circuit SCUBA gear.

Physico-chemical profile

The standing physico-chemical environment in Bundera Sinkhole has been reported in detail, including the nitrogen species profile, the polyphasic distribution of hydrogen sulphide and stable isotope distribution amongst the fauna (Humphreys 1999). Here only those parameters recorded by the sonde are considered as they were repeatedly recorded over a period of four days.

The water column had a strong physico-chemical stratification, with the different parameters exhibiting different types of stratification. These initial conditions as recorded during the first dive of the series are given here without further comment. There was a sharp thermocline with the temperature increasing with depth in the cave (Fig 2A) and a halocline not concordant with the thermocline (Fig 2B) with the upper brackish water overlying water close to seawater salinity. The pH declined from greater than 7.5 at the surface to *ca.* 6.9 at *ca.* 8 m at the bottom of the thermocline (Fig 2C). pH was lower in the upper water during the afternoon than in the morning, the pH 7.0 contour being 0.6 m deeper in the afternoon (8.6 m) than in the morning (8.0 m; P=0.021; Table 1), probably reflecting the photosynthetic activity in the photic zone; it was the only parameter showing a significant effect of time of day. The DO profile was polyphasic rapidly falling from supersaturated at the surface to a minimum at about 7.5 m depth followed by additional minima at *ca.* 17 m and 27 m depth (Fig 2D). The redox profile was also polyphasic (Fig 2E), ranging from -125 mV to +175 mV, and loosely concordant with both the DO profile (Fig 2F) and the upper two minima with elevated levels of hydrogen sulphide (Humphreys 1999).

Microbiotic environment

At high water in the sinkhole, the attached algae are submerged and the water appears clear, while at low water the algae spread over the water surface and impede

Table 1

The depths at which values of physico-chemical parameters are reached in Bundera Sinkhole for rebreathing diving (Closed) and subsequent open circuit or SCUBA diving (Open). Statistics are one-tailed Mann-Whitney U test.

	Closed	Open	n_1, n_2	U	P
Temperature 22 °C	-7.3 m	-6.7 m*	6,3	18	<0.025
Temperature 25 °C	-8.3 m	-8.7 m*	6,3	16.5	<0.05
Temperature range	1.1 m	2.0 m*	6,3	18	<0.025
Salinity 19 g L-1	-6.1 m	-4.5 m	6,3	18	<0.025
Salinity 32 g L-1	-15.9 m	-15.1 m*	6,3	17.5	<0.025
Salinity 19-32	-9.9 m	-10.6 m*	6,3	15.5	<0.1
DO 1.0 mg L-1	-4.6 m	-7.3 m*	3,3	9	0.05
DO 1.0 mg L-1	-8.9 m	-9.2 m*	3,3	6.5	ns
DO 2.5 mg	3.6 m	4.6 m*	3,3	9	0.05
pH 7.3	5.1 m	-4.3 m*	6,3	13.5	ns
pH 7.0	-8.2 m	-8.3 m*	6,3	9.5	ns
pH 7.3-7.0	-3.0 m	-4.7 m	5,2	10	0.05

* no significant regression of variable on time if the open circuit diving is excluded, indicating minor effect of closed circuit diving.

light penetration. Hence, the penetration of light into the deep algal layer will vary with both solar (diurnal) and lunar cycles, the latter having both a semi-diurnal and 14-day periodicity. This variation in light intensity will have some impact on the photic environment of the photosynthetic algae and bacteria and the resultant balance of photosynthesis and respiration in the upper photic zone of the cave. However, the marked thermocline will partially isolate the lower cave environment from these effects, which, nonetheless, deserve further examination. Humphreys (1999) provides evidence for the presence of a complex microbiotic environment in Bundera Sinkhole, near the thermohalocline, involving dense growths of sulphur and nitrifying chemoautotrophic bacteria, similar to that reported for comparable system in Quintana Roo, Mexico (Pohlman *et al.* in press).

Effects of diving

The gross form of most of the physico-chemical profiles changed little during successive dives with rebreathers, over four days in 1997, although there was a tendency for the sharp stratification at the initial thermohalocline to become less distinct with the interface thickening slightly. These changes through time are examined in more detail to determine in what manner the profiles change, and whether there is a significant difference between changes for closed (rebreathers) and open (SCUBA) circuit diving equipment (Table 1).

Temperature. The position of the 22 °C isotherm moved upwards (7.3 m to 6.7 m) while that of the 25 °C isotherm moved downwards (8.3 m to 8.7 m bws; Table 1) resulting in the zone of water between 22 °C and 25 °C increasing in thickness from 1.1 to 2.0 m (Table 1), thus making the thermocline less distinct.

Salinity. The position of the 19 g L^{-1} and 32 g L^{-1} haloclines both moved upwards, from 6.1 m to 4.5 m bws and from 15.9 to 15.1 m bws respectively, so that the position rather than the thickness of this salinity band changed (Table 1).

Dissolved oxygen. The position of the upper 1.0 mg L^{-1} DO isocline moved downwards, being at 4.6 m bws during the closed circuits dives and falling to 7.3 m bws after the open circuit dives (Table 1), while the lower 1.0 mg L^{-1} DO isocline did not change over time, remaining at *ca.* 9 m bws). There is an apparent step effect here with a major change in level associated with open circuit diving (after 65 hours; Fig 2F). Similarly the position of the upper 2.5 mg L^{-1} DO isocline moved downwards from 3.6 m to 4.6 m bws (Table 1).

The location of the lower 1.0 mg L^{-1} layer did not change with treatment (Table 1), suggesting that the cause of the surface mixing is replacement of oxygenated water downwards rather than the exhalant air itself oxygenating the water i.e. a result of turbulence rather than a direct reoxygenation. The movement of the upper 1.0 mg L^{-1} DO isocline to deeper water is especially significant because the more highly oxygenated water is intruding right through the upper hydrogen sulphide layer (Fig 2) which, from the evidence of the redox profiles (Fig 3A), was lost by the last dive. This intrusion of oxygenated water into this normally stable anoxic zone is likely to be of significance as this is the zone where the chemoautotrophic production is probably occurring (Humphreys 1999) and where the massive (presumed sulphur) bacteria colonies were disrupted after the first visit.

The general form of the DO depth profile changes quite subtly through time with some structure having been lost from the profile, especially in the lower sector, by the end of the field work (Fig 3B).

pH. The location of neither pH 7.0 nor pH 7.3 changed significantly with time or with treatment ($P = 0.92$ and $P = 0.26$ respectively) but the location of pH 7.0 and pH 7.3

Table 2

Between year comparison of temperature, salinity and pH at three depths in Bundera Sinkhole. The data are derived from three different sondes and from water chemistry data (see methods of Yager & Humphreys 1996). WC denotes water samples collected in bottles by divers.

	Temperature			Salinity				pH			
Depth m	1994 sonde	1995 sonde	1997 sonde	1994 WC	1994 sonde	1995 sonde	1997 sonde	1994 WC	1994 sonde	1995 sonde	1997 sonde
0.2	28	22.9	22.7	20	20.2	20	18.5	8.08	-	8.1	7.89
6	25.3	22.8	21.2	20	23.1	20	18.7	7.44	-	8.05	7.30
14	26.2	26.5	26.2	26.5	31.8	26.5	30.2	7.27	-	7.6	6.88

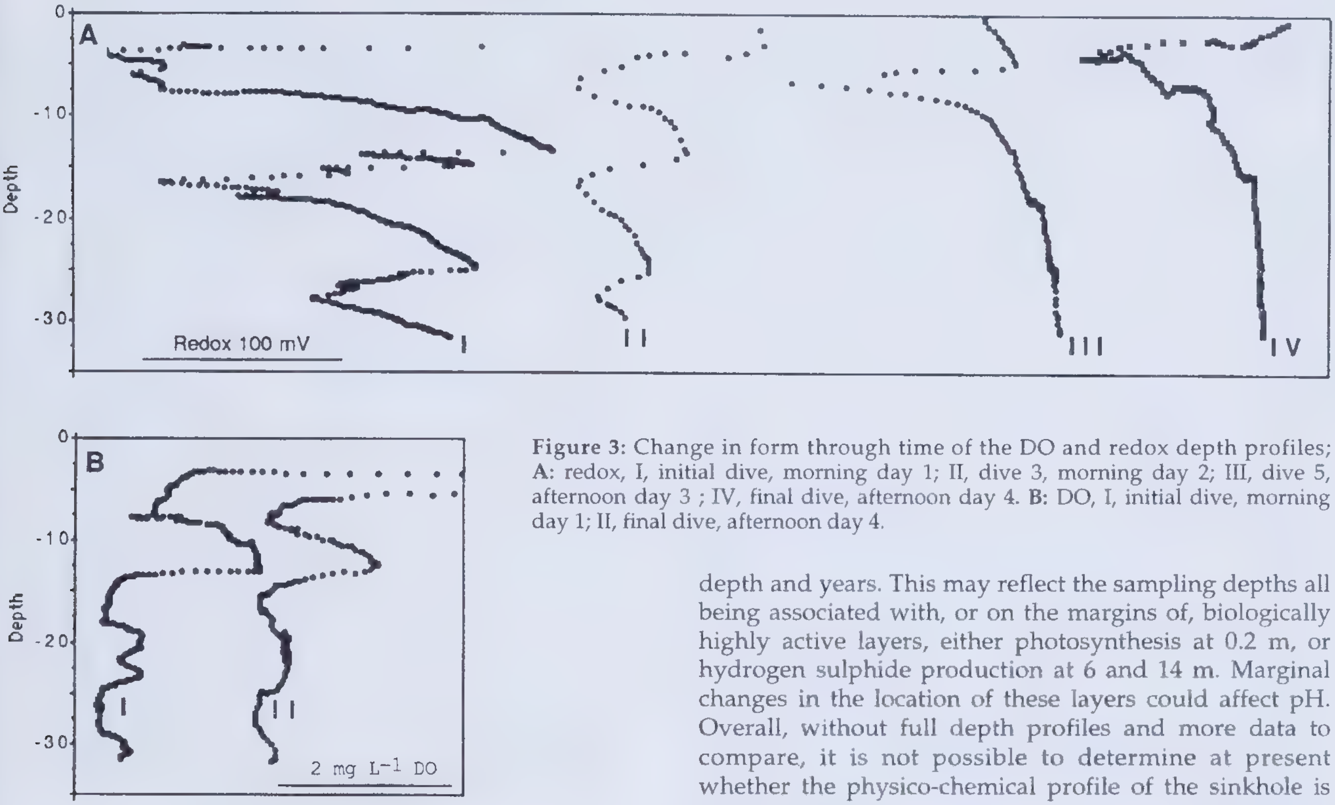

Figure 3: Change in form through time of the DO and redox depth profiles; **A:** redox, I, initial dive, morning day 1; II, dive 3, morning day 2; III, dive 5, afternoon day 3 ; IV, final dive, afternoon day 4. **B:** DO, I, initial dive, morning day 1; II, final dive, afternoon day 4.

diverged during the work with the range being significantly greater (P = 0.014) in the open circuit period (Table 1).

Redox. The redox profile was initially strongly polyphasic (Fig 3A) but both its general form and magnitude changes markedly through time, with most of the structure having been lost from the profile, especially in the lower sector, by the end of the field work. Overall, the minimum redox value recorded each dive increased through time ($Fs_{1,7}$ =9.63, P = 0.017). This effect is not associated with time of day or state of the tide as dives were conducted in the morning and afternoon (and thus also at different tidal states) over four successive days (caption to Fig 3).

Changes between years

Complete depth profiles are available only for the 1997 sampling, but some data can be compared from three specific depths for 1994, 1995 and 1997 (Table 2). The high temperatures of 28 °C and 25.3 °C at the surface and 6 m in 1994 result from this record having been made in the hotter season (March), while the remaining readings were made in the cooler seasons. Hence, the thermal stratification in the water column of Bundera Sinkhole is much less marked in the warmer seasons. However, at a depth of 14 m the water temperature is effectively constant between years.

The salinity at the surface and at a depth of 6 m is remarkably constant between years given that it should be influenced by local rainfall. However, the deep salinity varied by 20%, but this variation could be attributed to quite modest errors in the depth of sampling (especially the water bottle sample, in 1994) given the steep salinity gradient at this depth. pH values are variable between depth and years. This may reflect the sampling depths all being associated with, or on the margins of, biologically highly active layers, either photosynthesis at 0.2 m, or hydrogen sulphide production at 6 and 14 m. Marginal changes in the location of these layers could affect pH. Overall, without full depth profiles and more data to compare, it is not possible to determine at present whether the physico-chemical profile of the sinkhole is stable over time.

Both the distribution and abundance of the fauna differ between years, although little systematic sampling has been conducted (Table 3). This is especially noticeable in the main targets of the fauna sampling (*Lasionectes*

Table 3

Numbers of specimens taken or seen during the research dives as an indication of the changes to the biota in Bundera Sinkhole. + denotes presence, - denotes absence in samples. The location of the samples with respect to the thermohalocline is indicated.

	Below thermo-halocline	1993	1994	1995	1997
Below only					
Lasionectes	+	3	1	3	2
Danielopolina	+	1	-	41	1^2
Liagoceradocus	+	-	-	17	4^2
Polychaeta	+	-	1	3	-
Above and below					
Milyeringa	+	-	$+^3$	+	$+^1$
Stygiocaris	+	2	1	-	6
Other ostracods	-	+	+	+	+
Copepods	-	+	+	+	-
Above only					
Diptera	-	15	2	-	-
Mollusca	-	+	+	+	+
Other ostracods	-	+	+	+	+
Copepods	-	+	+	+	-

[1] Numerous *Milyeringa* counted by diver (see Humphreys 1999: Fig 3B). [2] A much greater effort was made to sample fauna in 1997 than in 1995 and resulted in the finding of several new taxa, so the apparent change in numbers is probably real. [3] Numerous *Milyeringa* counted at the bottom of the sinkhole from video recording taken by diver.

Table 4

Comparison of various physico-chemical parameter values from a number of anchialine caves. The range of values recorded is given. Some DO values are given in percent saturation (denoted %). Many of the data are plotted as profiles in Iliffe in press.

Location	Depth m	Temp. °C	Salinity $g L^{-1}$	pH	DO $mg L^{-1}$	REDOX mV	Reference
Bundera	32	21.1-26.4	18.5-34	6.88-7.4	0.2-6.9	-120 to +115	this paper
Bundera	21	22.8-26.7	20-27	7.6-8.1	1-3	-	this paper
Cueva de los Carboneros, Cuba	28	25.4-29.9	0-36.5	7-8.2	0.1-7.98	-273 to +97	Yager 1994
Church Cave, Bermuda	20	16-20	22-36	-	50-100%	-	Iliffe *et al.* 1984
Government Quarry, Bermuda	20	17-21	18-36	0-90%	-	-	Iliffe *et al.* 1984
Mayan Blue Quintana Roo, Mexico	22	25.2-26.0	3-34	6.6-7.2	0.9	1.65	Pohlman *et al.*, in press
Movile Cave, Romania	-	20.9	-	7.29	-	-341	Sarbu in press.
Wonderland Cave, Bermuda	10	21.7-23.1	24-36	7.34-7.67	3.8-6.8	-	Iliffe *et al.* in press.
Cueva de los Carboneros, Cuba	31	25-30.5	3-37	7.1-8.15	0.1-6.2	-	Yager 1994

exleyi, *Danielopolina* sp and *Liagoceradocus branchialis*) and in the conspicuous fauna, namely the blind fish *Milyeringa veritas*. Some species have only ever been recorded below the thermo-halocline (*e.g.* *L. exleyi*, *Danielopolina* sp and *L. branchialis*), while others are recorded throughout the water column but the vertical distribution of which differs markedly between years (*M. veritas*). In 1994, there was a large concentration of the fish at the extreme depth of the cave, while they were entirely lacking from this area in 1997 when they were at concentrations just below the thermocline (*ca.* 10 m) and at *ca.* 20 m (Humphreys 1999; Fig 3B), between the H_2S layers (Fig 2). This change in location of the principle predator (Humphreys & Feinberg 1995) suggests that the system is not stable.

The consequences of disruption to the physico-chemical stratification of the water column in the sinkhole are unknown, but it is pertinent to mention that remipedes globally have only ever been sampled below a thermo-halocline, always by cave divers in anchialine systems (Yager & Humphreys 1996). Hence, it is reasonable to expect that the loss of the thermo-halocline would be detrimental to the community. Secondly, breakdown of the physico-chemical stratification is likely to lead to the disruption of the biogeochemical processes associated with it.

Comparison with other areas

Most anchialine systems have a freshwater lens overlying sea water (Iliffe in press). This freshwater lens may be thick and increase in depth inland; for example, on the Yucatan Peninsula 2 km inland it is 10 m thick at sinkhole Abejas and 10 km inland it is 20 m thick at sinkhole Vaca Ha (Iliffe in press). At Wonderland Cave, Bermuda, brackish water overlies seawater, and this cave is most similar to Bundera Sinkhole in its salinity profile (Iliffe in press: Fig 3).

A summary of published physico-chemical profiles of anchialine systems (Table 4) indicates that Bundera Sinkhole is the deepest of these and probably the smallest. In Bundera Sinkhole there is a polymodal DO depth profile, unlike any other DO depth profile, each of which exhibits a unimodal DO depth profile. By inference, this suggests that the other systems probably have a single H_2S layer.

The physico-chemical environment in the Bundera Sinkhole is very complex (Humphreys 1999) and this complexity is associated with biogeochemical processes that are likely to be of fundamental importance to the maintenance of the unique community contained in this anchialine cave. SCUBA diving clearly disrupts the vertical stratification of the physico-chemical environment in Bundera Sinkhole and this may affect the unique anchialine community inhabiting the cave. As some of the fauna associated with such anchialine systems have only ever been collected by divers (*e.g.* remipedes) then diver access is essential for biological work. However, diving should be restricted and, where possible, conducted using rebreathing equipment. There is a lack of basic data on the gross physico-chemical environment in the sinkhole on groundwater movement, temporal changes in the profile resulting from the effects of episodic rainfall on surface input, as well as groundwater flow. A diver-free profiling system would be ideal to establish the long term changes in the sinkhole, particularly the establishment and maintenance of the complex redox profile, its associated chemolithotrophic organisms and the significance of these processes to the remipede community.

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A new genus and two new species of Hydrobiidae (Mollusca: Gastropoda: Caenogastropoda) from south Western Australia

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Abstract

A new genus of hydrobiid gastropod, *Westrapyrgus* n gen, containing two new species, is described from south Western Australia, these species being the first freshwater members of this family to be described from this state. One species, *W. westralis* n sp, is found in coastal springs in the south-west of Western Australia; the other, *W. slacksmithae* n sp, is from the Avon and Moore Rivers, to the north-east of Perth. The new genus is morphologically most similar to the south-eastern Australian freshwater genus *Austropyrgus* and to the estuarine genus *Tatea*.

Introduction

Freshwater snails of the family Hydrobiidae have recently been shown to be diverse in Australia with large faunas in south-eastern Australia, especially in Tasmania (Ponder *et al.* 1993; Clark, Ponder & Miller unpubl. observ.) and in artesian springs associated with the Great Artesian Basin (Ponder *et al.* 1989, 1995; Ponder & Clark 1990; Ponder 1995). A number of these species are listed as threatened by the International Union for the Conservation of Nature (Baillie & Groombridge 1996; Ponder 1994, 1997, 1998). Many hydrobiids show small morphological differences between populations, even in those from adjacent drainages (*e.g.* Ponder 1982; Ponder *et al.* 1993) and these differences are often indicative of marked genetic differentiation (Colgan & Ponder 1994; Ponder *et al.* 1994, 1995, 1996). To complicate matters further, cryptic species are known to occur in sympatry (Ponder *et al.* 1994).

Apart from Kendrick's (1976) record of *Potamopyrgus* sp from the Avon River, to date the only published valid records of the family Hydrobiidae from Western Australia are for estuarine species in the genera *Ascorhis* (Ponder & Clark 1988) and *Tatea* (Ponder *et al.* 1991). Recently Davis & Christidis (1997) recorded *Potamopyrgus* sp from the Perth area but this record is erroneous, being based on a species of *Coxiella*, a member of the Pomatiopsidae. Nevertheless freshwater hydrobiids associated with coastal springs in the south-west of Western Australia and the River Avon north-east of Perth (Kendrick 1976) have been known for many years (G W Kendrick and S M Slack-Smith, pers. comm.) but have remained undescribed until now.

Material and Methods

Collection

Material for this project was obtained from existing museum collections (see list in Abbreviations), or collected either by hand, by picking from the surface of the substratum, by washing submerged stones, wood and vegetation, or by sweeping vegetation with a hand sieve. Specimens were, in some instances, relaxed using menthol crystals. The samples were then fixed in 10 % formalin neutralised with sodium bicarbonate and, after sorting, stored in 5 % buffered seawater formalin. Where sufficient material was available a sub-sample from each lot was dried.

Morphology

Shells, opercula and radulae were mounted using standard techniques (*e.g.* Ponder *et al.* 1993) and, for the type species, the head-foot was critical-point dried as described by Ponder *et al.* (1993). They were then examined after coating with gold using a Cambridge Instruments S120 scanning electron microscope (SEM). Three radulae were examined for each species.

Using specimens from the type series, shells and opercula were measured using a digitising pad linked to a computer, as described in detail by Ponder *et al.* (1989). The measurements taken are listed below under Abbreviations and all are given in mm. The convexity ratio (CV) is detailed in Ponder *et al.* (1989: Fig 4B). It is calculated using the distance from the outer edge of the middle of the whorl to a line connecting the sutures divided by the distance between the sutures at the end of the penultimate whorl. The number of whorls was counted using the method illustrated in Hershler & Ponder (1998: Fig 17m). Opercular peg length is the vertical height of the longest peg, but not necessarily the same peg in all individuals even within the same species (see Ponder *et al.* 1989: Fig 4E).

Some of the specimens used for measurement were utilised for dissection. Dissection was carried out by one of us (SAC) using an Orient SM1 stereomicroscope and drawing apparatus with the animal in a black, solid watch glass. Fine watchmakers' forceps were used and the specimen being dissected was immersed in tap water containing a few drops of Bouin's fixative to improve contrast. Three specimens of each sex were dissected of

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both species. The characters were scored according to a predetermined list of states similar to those employed by Ponder *et al.* (1993). Anatomical measurements were also made and are given in the Appendix. The type species was studied alive by one of us (WFP).

The descriptions were generated using DELTA (Dallwitz *et al.* 1993). The list of characters and their states can be obtained from the first author on request but are similar to those used by Ponder *et al.* (1993).

Statistical analyses were carried out using SYSTAT 5 (Wilkinson 1992). Shell, opercular and anatomical measurements were subjected to ANOVA. Discriminant function analysis was used to test the robustness of the species groups. Sexual dimorphism in shell size (shell length and width) was tested by t-test. A probability > 0.01 was considered to be non-significant.

Abbreviations

Institutions: AMS, Australian Museum, Sydney; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth.

Shell measurements and counts: AL, aperture length; AW, aperture width; BW, length of last (body) whorl; CV, convexity ratio; SL, shell length; SW, shell width; TW, number of teleoconch whorls.

Opercular measurements and counts: ML, length of white smear; OL, opercular length; OW, opercular width; PH, maximum peg length; PL, length of area occupied by pegs; PN, number of pegs.

Taxonomy

Family Hydrobiidae

Subfamily Tateinae

Recent studies have enabled a clarification of the generic groupings that have appeared in recent literature and these are briefly outlined below and summarised in Table 1. Ponder (1982) listed as synonyms of *Hemistomia* Crosse, 1872 (type species *H. caledonica* Crosse, 1872) four genus-group names from Australia - *Fluvidona* Iredale, 1937 and *Rivisessor*, *Pupiphrix* and *Angrobia* all of Iredale, 1943, although he did suggest that several groups were present that "may represent subgenera within *Hemistomia* or even separate genera". Ponder (1988) later showed that *Paludina nigra* Quoy and Gaimard, 1835, the type species of *Austropyrgus* Cotton, 1942 (see Cotton, 1942 and Ponder, 1988 for the type species designation) was a species of the group then recognised as *Fluvidona* Iredale, 1943. Recent work on the New Caledonian taxa, including *H. caledonica*, indicates that they can be regarded as distinct from the Australian radiation (Haase & Bouchet 1998). The use of *Fluvidona* for the Australian taxa was followed by Smith (1992) and Ponder *et al.* (1994). However, subsequent work (Miller *et al.* 1999) has shown that *Fluvidona* Iredale, 1937 (type species *Hydrobia petterdi* Smith, 1882), which includes several species in northern New South Wales and southern Queensland, is demonstrably distinct from the large group of species found in south eastern Australia and Tasmania which is now referred to *Austropyrgus*, this latter genus-name including *Rivisessor*, *Pupiphrix* and *Angrobia* as synonyms.

Westrapyrgus n gen

Derivation of name: *Westra* – derived from Western Australia, *pyrgus* Greek, a tower – adopted because of its use in the generic names *Austropyrgus* and *Potamopyrgus*. Gender masculine.

Type species: *Westrapyrgus westralis* n sp

Description

Hydrobiid with an almost smooth, conical shell; protoconch paucispiral with pitted to irregularly wrinkled microsculpture; teleoconch with fine axial growth lines and very fine spiral grooves. Aperture ovate, outer lip slightly to moderately thickened, not reflected. Operculum yellow, paucispiral, flat, with several short, white pegs on inner surface. Head-foot with long, tapering cephalic tentacles, pigmented along entire length or at bases only; pigment on rest of head-foot present or absent; mantle edge simple. Osphradium short, near posterior end of ctenidium; narrow, with pointed ends. Ctenidium well developed, with broad, triangular filaments. Radula similar to related genera (*e.g. Tatea*, *Austropyrgus*, *Fluvidona*) with central teeth each bearing 3-4 pairs of basal cusps. Stomach with posterior chamber markedly smaller than anterior, posterior caecum large, rounded, expanded behind stomach. Male with oval prostate gland with visceral portion slightly longer than pallial section. Pallial vas deferens undulating between prostate and base of penis. Penis on right side of head, with swollen base and longer distal portion. Penial duct undulating through swollen base of

Table 1

Summary of the recent nomenclatural history of the names *Austropyrgus* and *Fluvidona*. Valid genera shown in bold.

Ponder, 1982	Ponder, 1988; Smith, 1992; Ponder *et al.*, 1994	Miller *et al.* 1999 and this work
Hemistomia Crosse, 1872	***Hemistomia*** Crosse, 1872	***Hemistomia*** Crosse, 1872
Fluvidona Iredale, 1937	***Fluvidona*** Iredale, 1937	***Fluvidona*** Iredale, 1937
	Austropyrgus Cotton, 1942	***Austropyrgus*** Cotton, 1942
Rivisessor Iredale, 1943	*Rivisessor* Iredale, 1943	*Rivisessor* Iredale, 1943
Pupiphrix Iredale, 1943	*Pupiphrix* Iredale, 1943	*Pupiphrix* Iredale, 1943
Angrobia Iredale, 1943	*Angrobia* Iredale, 1943	*Angrobia* Iredale, 1943

penis and most of evenly-tapering distal part. Female reproductive system similar to other members of subfamily but with anterior ovary distinctly lobulate. Renal oviduct forms simple U-shaped loop. Seminal receptacle ovoid, distally rounded, with short duct. Bursa copulatrix large, globular, posterior to albumen gland. Albumen gland about equal in length to capsule gland, both glands swollen. Ventral channel (of capsule gland) terminates behind anterior end of capsule gland, pallial genital opening behind anterior end of ventral channel, placed sub-terminally to almost centrally. Renal organ and pericardium extend for about half their length into mantle roof. Circum-oesophageal ganglia typical of family in configuration and unpigmented. Cerebral ganglia well separated (commissure nearly equal to width of ganglion), right pleural-supra-oseophageal connective slightly longer than length of supra-oesophageal ganglion; pedal ganglia short and rounded with short commissure.

Remarks

The two species included in the new genus resemble some species now included in *Austropyrgus* (*i.e.* Ponder *et al.* 1994 as *Fluvidona*) but differ in having pointed (not rounded) ends to the osphradium, the penial duct undulating through most of the length of the long distal part of the penis (not straight or undulating only in basal half or less of distal part) and the female genital opening located well behind the anterior end of the capsule gland (about $^1/_3$ to $^1/_2$ length of the gland from the anterior end, not anterior to the capsule gland, or near terminal). The teleoconch differs in possessing very fine spiral grooves over the whole surface, this character not having been seen in more than 70 species of *Austropyrgus* (Clark, Ponder and Miller unpubl. observ.). In most other characters the two genera are very similar (protoconch, teleoconch shape, general anatomy, operculum). *Westrapyrgus* is most similar to *Tatea* in the characters of the female reproductive system (Ponder *et al.* 1991) but differs from that genus in having a paucispiral protoconch with wrinkled, not spiral microsculpture; a more broadly conical shell covered with minute spiral grooves; in the cephalic tentacles lacking a distal dark band and ciliated ridges on the proximal part of the right tentacle; and in lacking a markedly thickened shell aperture. Again, in the general features of the anatomy, operculum and radular characters, *Tatea* is very similar to *Westrapyrgus* but this is also true for many of these presumably plesiomorphic characters for other members of the subfamily Tateinae (*Fluvidona, Potamopyrgus, Hemistomia, Fluviopupa* etc).

Westrapyrgus westralis n sp

Figs 1A-C; 2A; 3A,B; 4A,B; 5A,B, E, F; 6.

Material Examined

Holotype and Paratypes. 'The Spring', off Skippy Rock Rd, Leeuwin-Naturaliste National Park, WA, 34° 20.98' S 115° 09' E, alt: 20-40 m, 15 Aug 1982, on water cress, coll P H Colman. AMS, C.340714 (Holotype), C.201006 (many paratypes), C.307579 (3 figured paratypes). WAM (S.12386) (5 paratypes).

Additional Material. Cape Leeuwin, adjacent to water reserve swamp, 34° 22' S 115° 7.98' E, coll O Schatz, pres: E V Finckh Coll, 1971, AMS, C.201008 (5); same locality, in water race, on sides of channel, WA, alt: 20-40m, 15 Aug 1982, coll P H Colman, AMS, C.201005 (many); same location, 12 Jan 1982, coll I Loch, AMS, C.201007 (many); same location, coll S Slack-Smith & B R Wilson, 24 Mar 1975, WAM 766-82 (many); Quarry Bay, Cape Leeuwin, WA, 34° 22' S 115° 08' E, from natural spring flowing from hillside, amongst watercress, coll A Brearley, 22 Jan 1978, WAM 765-82 (many).

Ellen Brook Homestead at Ellen Brook, WA, 33° 57' S 115° 01' E, on damp and wet rock surfaces in splash zone of dam spillway, near homestead, coll G W Kendrick, 14 Sep 1980, WAM 752-82 (7); Ellen Brook, Leeuwin-Naturaliste National Park, 9 km NW of Margaret River townsite, waterfall, WA, 33° 54.83' S 115° 0.12' E, 29 Aug 1985, under rocks, on and above falls, coll W F Ponder, AMS, C.201012 (many); same locality, at and above entrance to Meekadarribee Cave, above & below water level, shaded by *Agonis* tree and Arum lilies, coll M Ellis and S Slack-Smith, 13 Oct 1980, WAM 753-82 (many); same locality, edge of spring-fed stream ca 20 m upstream from Meekadarribee waterfall, on moist soil under litter on edge of stream, WAM (many);

"Glenbourne", 33° 54.83' S 115° 0.65' E, spring in tributary on N side, ca 1.5 km W from Caves Road near base of limestone cliffs, 29 Aug 1985, on wood, surface and debris, coll W F Ponder, AMS, C.201010 (many); same locality, coll G W Kendrick, 25 Dec 1976, WAM 811-80 (many); same locality, coll G W Kendrick, 14 Jan 1982, WAM (many); "Glenbourne", 33° 54.97' S 115° 0.05' E, 29 Aug 1985, tributary on N side, ca 1.5 km from main road near junction with main creek, coll W F Ponder, AMS, C.201011 (many).

Yallingup, WA, 33° 39' S 115° 1' E, SAM, TD72 (many); same locality, AM C.202722(3).

Deepdene Cliffs, near Augusta, WA, 34° 16' S 115° 03' E, seepage area at foot of cliffs, coll M Archer, E Jeffreys *et al.*, 15 Nov 1969, WAM 758-82 (many); Turner Brook, Deepdene, near Augusta, WA, 34° 16' S 115° 03' E, coll M Archer, E Jeffreys *et al.*, 15 Nov 1969, WAM 754-82 (many); same locality, in stream coming from cliffs to rd, coll A Paterson, 12 July 1971, WAM 755-82 (many); south side of Turner Brook, near and below Deepdene Cliff, WA, 34° 16' S 115° 03' E, steep bank, leaf litter below *Agonis flexuosa*, coll S Slack-Smith & M Ellis, 3 Aug 1980, WAM 757-82 (many) and 756-82 (10);

Augusta, WA, 34° 19' S 115° 09'E, caught in the filter of a water meter in the town, coll B J Fleay (Met Water Board), 1973, WAM 759-82 (many); same locality, in filters of town water supply, coll R Curtis (Dept of Health), July 1976, WAM 760-82 (many).

Creek at Marlamup Beach, NW of Windy Harbour, 3 km from Black Head, WA, 34° 44' S 115° 57' E, spring at base of limestone cliffs at junction with ferrugineous rocks and gneiss-bassalt flows, coll B Muir, 5 May 1981, WAM 301-82 (many).

Moses Rock, 15 km NW of Cowaramup, WA, 34° 28' S 116° 15' E, in spring stream below Quininup Lake Cave (CO1), 33° 44' S 115° 02'E, coll V A Ryland, 19 Apr 1976, WAM (many); same locality, in edge of lake below

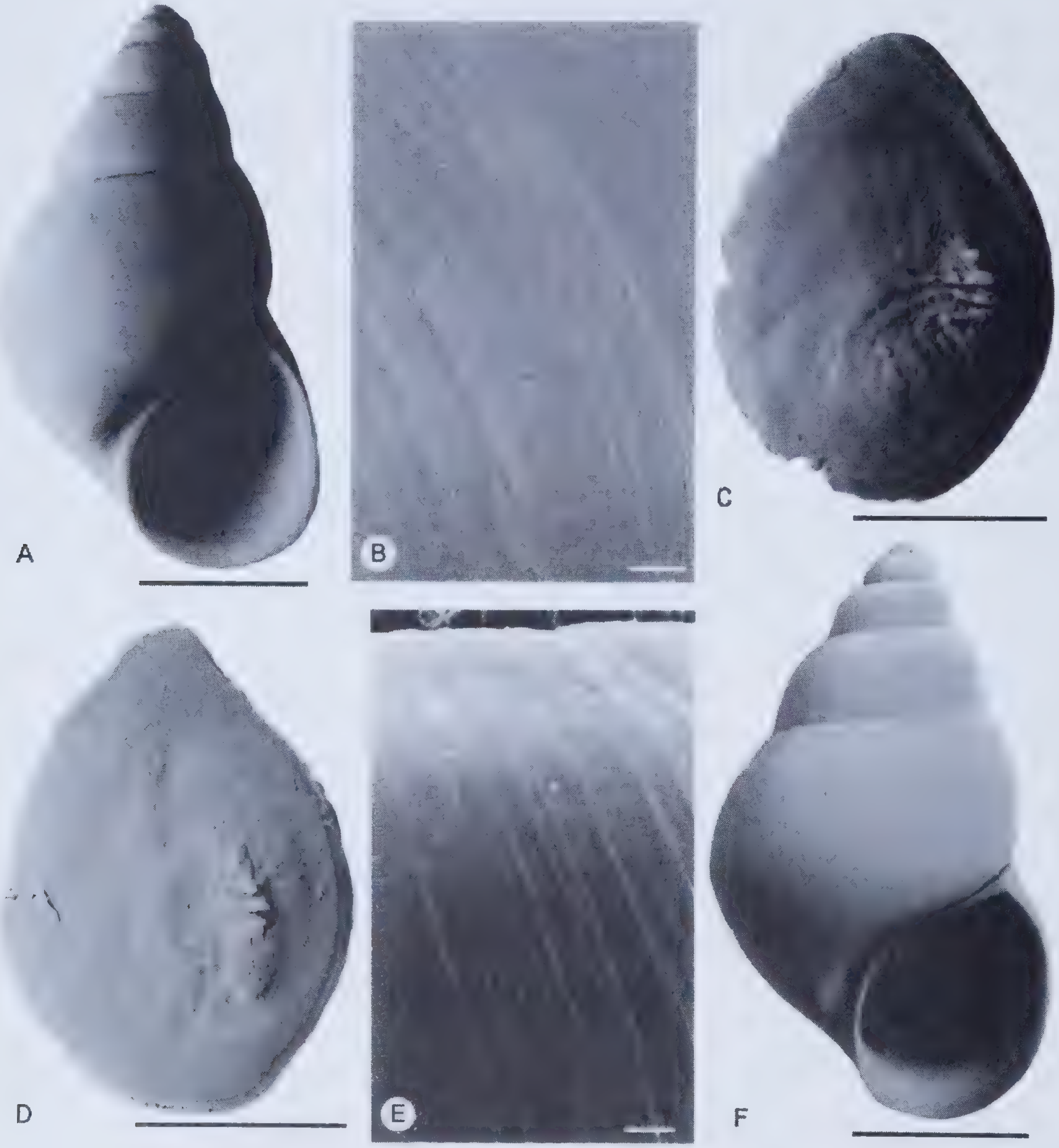

Figure 1. Shells and opercula of *Westrapyrgus* species. **A-C.** *Westrapyrgus westralis* n sp. **A,** shell of holotype. **B,** microsculpture on first quarter of last whorl. **C,** operculum, inner surface (paratype). **D-F.** *Westrapyrgus slacksmithae* n sp. **D,** shell of holotype. **E,** microsculpture on first quarter of last whorl. **F,** operculum of paratype, inner surface. Scales: A, B 1mm; C 200 µm; D 300 µm; E, F 500 µm.

Quininup Lake Cave (CO1), coll V Ryland, 19 Apr 1976, WAM (many).

Creek (Weld River?) flowing into Broke Inlet, WA, 34° 56' S 116° 27' E, coll B G Muir, 26 Oct 1967, WAM (1 juvenile, broader and probably larger than the other material, with marked peripheral angulation).

Diagnosis

Shell conical, whorls weakly convex, periphery subangled; head-foot unpigmented; penis with elbow in middle of distal part when at rest; pallial opening of female genital system placed at about middle of capsule gland and behind anterior end of ventral channel.

Description

Shell (Figs 1A,B; 2A; 3A,B; Table 2). Up to about 4.2 mm in length, spire outline straight. Protoconch (Fig 3A,B) of about 1.3 whorls, with wrinkles forming close, irregular pits (Fig 3B). Teleoconch of up to 4.8 slightly convex whorls, last whorl and base evenly convex to weakly subangled. Surface with fine orthocline growth lines and very fine spiral grooves (Fig 1B). Inner lip of aperture firmly adhering to parietal wall, outer lip weakly to moderately thickened. Colour yellow-brown, semi-translucent to opaque.

Table 2

Shell dimensions of holotype and paratypes (n = 20; minimum, maximum, mean, standard deviation) of *Westrapyrgus westralis* (in mm).

	SL	SW	AL	AW	BW	CV	TW
Holotype	3.24	1.92	1.32	1.16	2.32	0.14	3.8
Paratypes							
Min	3.02	1.80	1.21	1.03	2.18	0.10	3.8
Max	4.13	2.33	1.60	1.34	2.90	0.16	4.8
Mean	3.46	2.04	1.42	1.19	2.45	0.13	4.2
sd	0.30	0.15	0.11	0.08	0.20	0.02	0.2

Sexual dimorphism. Males (n = 4) are smaller than females (n = 16) in shell length (males 3.14 ± 0.11 mm, females 3.54 ± 0.28 mm) and width (males 1.89 ± 0.06 mm, females 2.08 ± 0.14 mm) and, although these differences are significant (t-test, $P< 0.01$) the results are inconclusive because of the small number of males measured.

Operculum (Fig 1C). With 2-4 pegs on inner surface, pegs occupying 0.15-0.36 of opercular length (0.24 ± 0.05mm).

Table 3

Opercula dimensions of paratypes (n = 20; minimum, maximum, mean, standard deviation) of *Westrapyrgus westralis* (in mm).

	OL	OW	ML	PL	PH	PN
Min	1.03	0.79	0.20	0.15	0.16	2
Max	1.34	0.99	0.45	0.48	0.36	4
Mean	1.18	0.86	0.31	0.29	0.21	3.20
sd	0.09	0.05	0.06	0.07	0.05	0.70

Radula (Fig 4A,B). Central teeth: each with 4-5 lateral cusps, median cusp of medium width, sharply pointed, about 1.5 times longer than adjacent cusps; 3-4 pairs of basal cusps. Basal tongue U-shaped, not protruding past

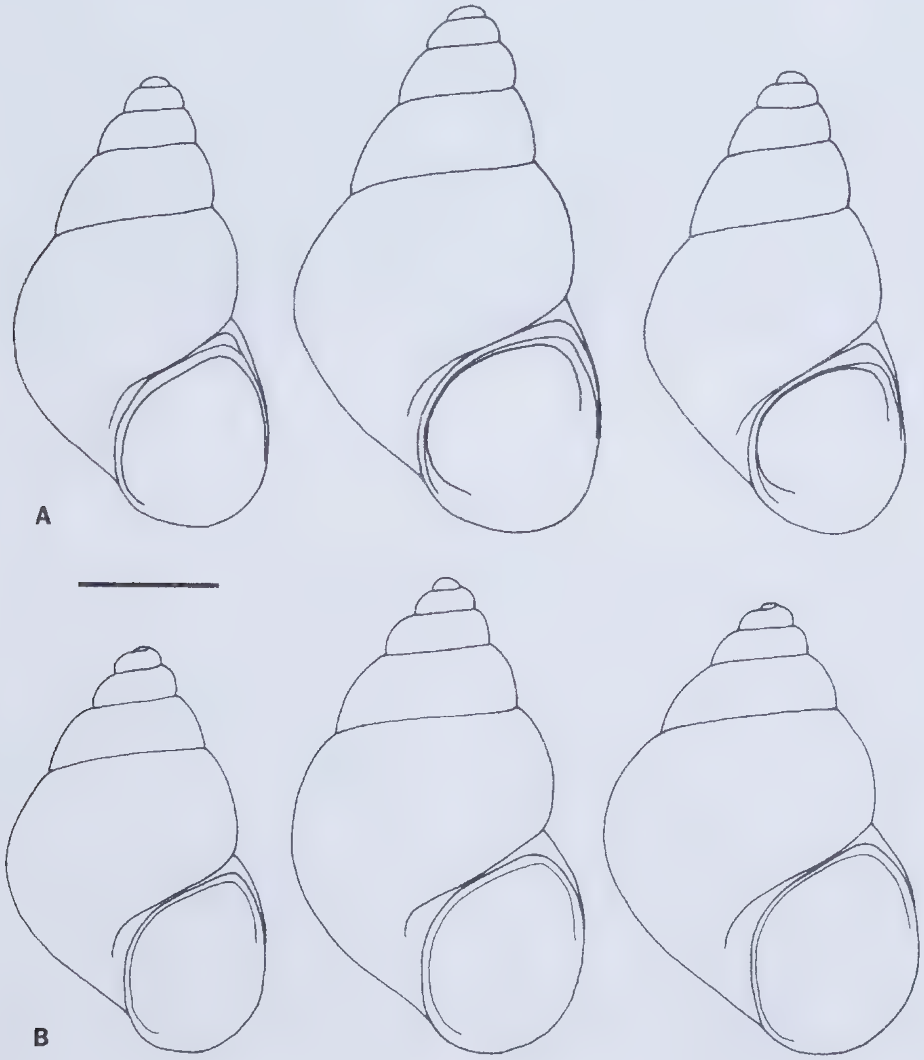

Figure 2. Shells of *Westrapyrgus* species. **A,** *Westrapyrgus westralis* n sp, shells of three paratypes (AMS, C.307579). **B,** *Westrapyrgus slacksmithae* n sp, shells of three paratypes (AMS, C. 340673). Scale 1 mm.

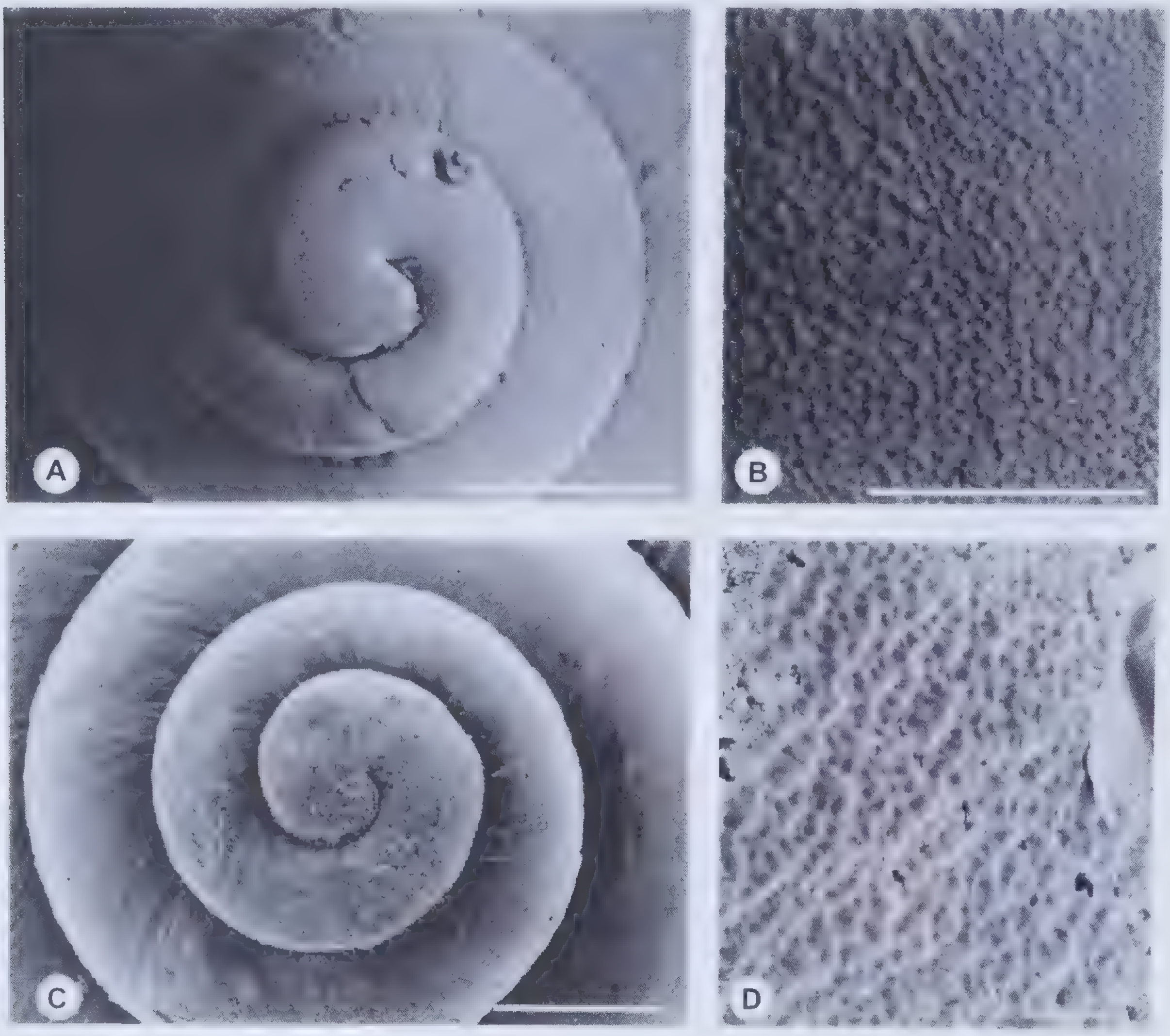

Figure 3. Protoconchs of paratypes of *Westrapyrgus* species. **A, B.** *Westrapyrgus westralis* n sp. **A,** protoconch and upper teleococh whorls. **B,** microsculpture of protoconch. **C, D.** *Westrapyrgus slacksmithae* n sp. **C,** protoconch and upper teleococh whorls. **D,** microsculpture of protoconch. Scales: A, C 200 µm; B, D 50 µm.

lateral edge. Lateral teeth: each with 4 cusps on both sides, median cusp sharply pointed; less than 2 times longer than adjacent cusps. Basal projection of lateral teeth bluntly pointed. Marginal teeth: inner with 20-25 cusps; outer with 30-37 cusps.

Head-foot (Fig 5E). Snout moderately long, anteriorly bilobed, unpigmented; with cilia in lateral groove behind labia. Foot 1.5 to twice as long as wide, with anterior edge straight to slightly indented and slightly expanded laterally, posteriorly rounded; largely unpigmented, some specimens with little grey pigment anterior to unpigmented opercular lobe. Cephalic tentacles long and tapering, with eyes in weak swellings at base; unpigmented except for grey to black pigment around eye; mid dorsal and mid ventral cilial tracts present and rather weak cilia on lateral edges. Head and neck unpigmented except for posterior continuation of pigment behind eye in some specimens. Cilial tract of right side, especially marked in females and some cilia on anterior parts of foot lateral to snout. Pallial roof and visceral coil unpigmented.

Anatomy (see Appendix for measurements).

Mantle Cavity. Ctenidium with 19-23 (n = 6) filaments, posterior most filament overlaps pericardium. Osphradium elongate, with pointed ends, located between posterior end and middle of ctenidium (posterior end of osphradium at about 3rd to 5th posterior ctenidial filament). Hypobranchial gland well developed; partly covering straight to slightly arched rectum. Renal organ extends forward *ca.* ½ its length into pallial cavity; pericardium more than ½ within pallial roof.

Stomach (Fig 5B) with large caecum.

Male Reproductive System (Fig 5E, F). Testis of 1.25-1.4 (n = 3) whorls. Seminal vesicle loosely coiled over stomach and conspicuously coiled on both digestive gland and testis behind stomach. About ⅓ of prostate gland within pallial roof, oval in shape, compressed in section. Pallial vas deferens flush with surface; slightly to strongly undulating between prostate and penis, strongly undulating at base of penis. Penis (Fig 5F) unpigmented, with expanded basal portion and distinct elbow about half way along elongate distal portion; proximal part of distal portion with parallel sides, distal part tapering.

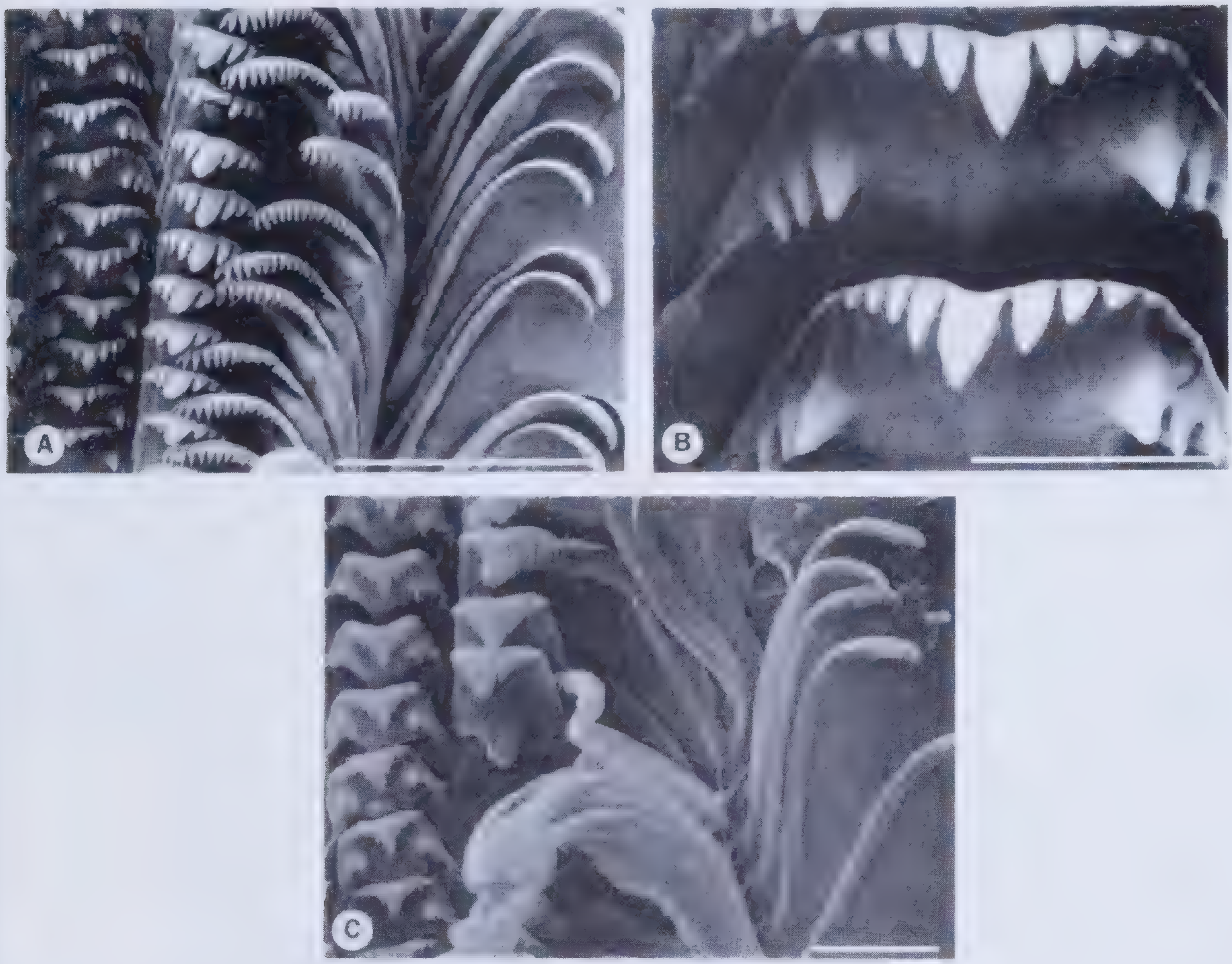

Figure 4. Radulae of paratypes of *Westrapyrgus* species. **A, B.** *Westrapyrgus westralis* n sp. **A,** half rows. **B,** detail of central teeth. **C,** *Westrapyrgus slacksmithae* n sp half rows. Scales: A 50 µm; B 10 µm; C 20 µm.

Penial duct undulating through basal part and about two thirds of distal portion.

Female Reproductive System (Fig 5A). Ovary of about 1.0-1.3 (n = 3) whorls. Coiled oviduct with initial U-shaped loop orientated dorso-ventrally; initial loop medium; proximal part simple with two bends; one bend distal to seminal receptacle. Coiled oviduct and bursal duct join at posterior pallial wall. Bursal duct parallel sided and straight. Oviduct joining bursal duct ventrally or from right side. Seminal receptacle with short duct, ovoid and located at anterior edge of bursa copulatrix. Rectum overlapping albumen and capsule glands. One quarter or less of albumen gland in front of posterior pallial wall. Capsule gland with anterior end tapering or rounded, compressed-oval in section, with distinct glandular zones. Ventral channel indistinct to distinct, with indistinct muscular vestibule; genital opening small; located nearly ½ way along capsule gland.

Etymology. Named after Western Australia.

Remarks

This species has been found in several coastal springs in south Western Australia (Fig 6) between Cape Naturaliste and the Weld River, and is locally abundant, even to the point where it has been found clogging water filters in Augusta. More extensive survey work in this area will probably increase the number of localities and perhaps extend the geographic range. Confirmation of the eastern-most record (stream flowing into Broke Inlet) is required as this is based on a single juvenile, which has a more strongly angled periphery than the other specimens. The species shows some variation in size within and between populations, one lot in particular (WAM 753-82) being markedly smaller than most others.

The paucity of pigment on the head-foot of this species is unusual, most surface species, like that described below, having a strongly pigmented head-foot.

This species has a similar distribution to that of another caenogastropod, *Austroassiminea letha* Solem *et al.* 1982, a species that is also restricted to coastal springs and seepages (Solem *et al.* 1982), and the two species are

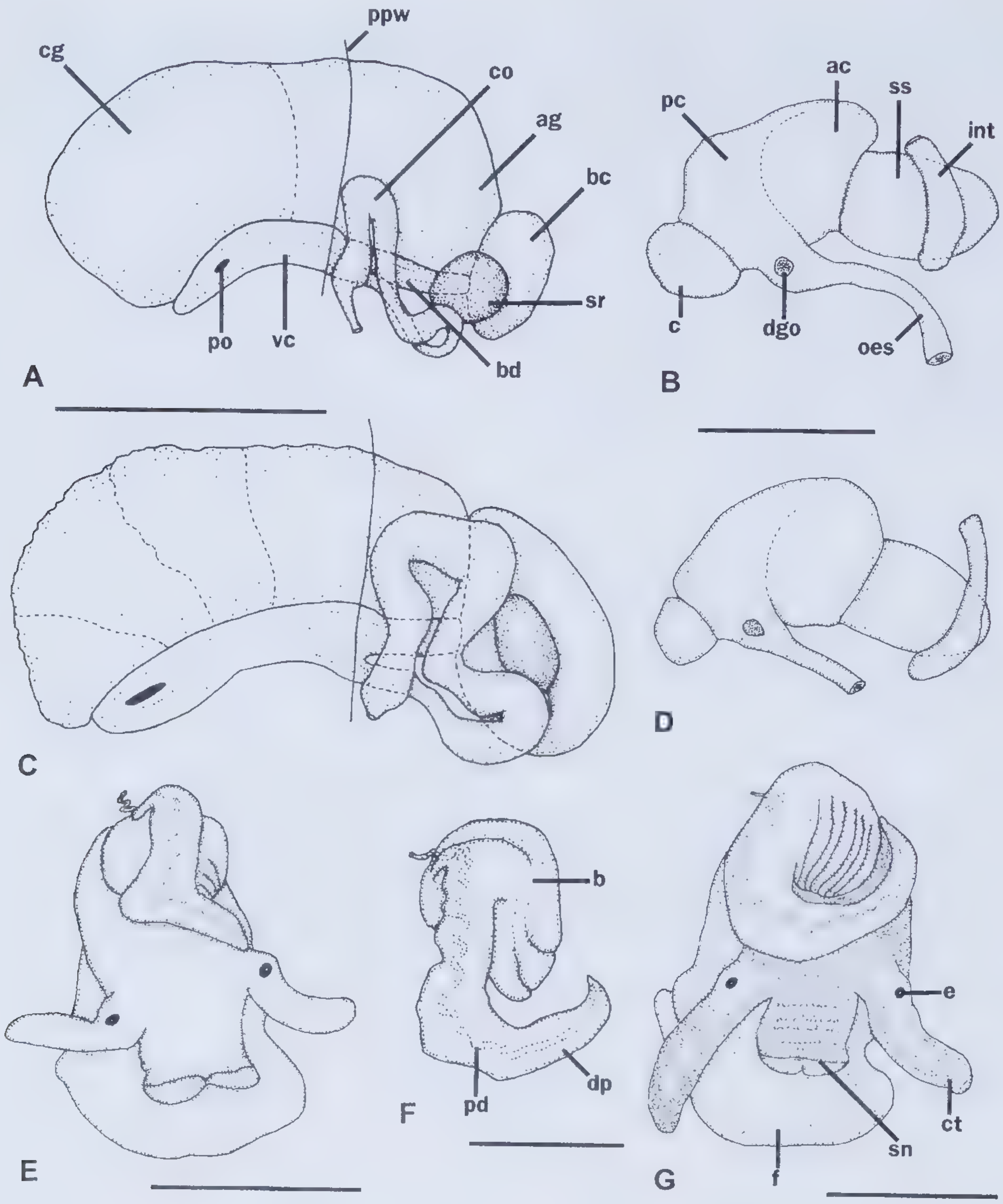

Figure 5. Anatomy of paratypes of *Westrapyrgus* species. **A,B,E,F.** *Westrapyrgus westralis* n sp. **A**, female genital system from left side. **B**, stomach. **E**, head of male showing penis. **F**, detail of penis. **C, D, G.** *Westrapyrgus slacksmithae* n sp. **C**, female genital system from left side. **D**, stomach. **G**, head of male showing penis. Abbreviations: ac – anterior chamber of stomach; ag – albumen gland; b – base of penis; bc – bursa copulatrix; bd – bursal duct; c – caecum of stomach; cg - capsule gland; co – coiled renal oviduct; ct – cephalic tentacle; dgo – digestive gland opening; dp – distal part of penis; e – eye; f – propodium of foot; int – intestine; oes – oesophagus; pc – posterior chamber of stomach; pd – penial duct; po – opening of pallial oviduct; ppw – position of posterior wall of pallial cavity; sn – snout; sr – seminal receptacle; ss – style sac; vc – ventral channel. Scales: A-E, G 0.5 mm; F 0.2 mm.

found together in two localities (Ellen Brook, Turner Brook near Deepdene Cliffs). Hydrobiids have not been recorded from Cosy Corner, the third locality where living *Austroassiminea* was found.

Westrapyrgus slacksmithae n sp

Figs 1D-F; 2B; 3C,D; 4C; 5C,D,G; 6.

Potamopyrgus sp

Kendrick 1976: 101, Fig 4, Table 1.

Material Examined

Holotype and paratypes. Walyunga Pool, Avon R, near junction of Woorooloo Brook and Avon River, at car park, Walyunga National Park, NE of Perth, WA, 31° 44' S 116° 05' E, 12 Sept 1987, among roots etc, coll W F Ponder & S. M. Slack-Smith, AMS, C.340715 (Holotype), C.340673 (3 figured paratypes), C.201013 (many paratypes), WAM (S.12387) (5 paratypes); Avon R, NE of Perth, 1 km upstream from parking area, Walyunga NP, WA, 31° 44' S 116° 04' E, 12 Sept 1987, in long pool, coll W F Ponder & S M Slack-Smith, AMS, C.201408 (7 paratypes).

Other material examined. Walyunga Pool, Avon R, Walyunga National Park, WA, 31° 44' S, 116° 05' E, coll S Slack-Smith, 5 May 1971, WAM 763-82 (3); same loc, coll S Slack-Smith & A Paterson, 3 May 1971, WAM 762-82 (4); Long Pool near Walyunga Pool, under sides of stones in shallows, coll G W Kendrick, 6 Feb 1969, WAM 764-82 (20); same loc, alive under stones in river bed, coll G W Kendrick, 12 Apr 1970, WAM 862-71 (7).

Moore River crossing, 6 miles E of Guilderton, WA, 31° 20' S 115° 33' E, on bark and sticks at stream edge, coll G W Kendrick, 2 Jan 1970, WAM 761-82 (3).

Diagnosis

Shell ovate-conic, whorls convex, periphery rounded; head-foot black or dark grey; penis with distal portion evenly curved; pallial opening of female genital system in anterior third of capsule gland and close to anterior end of ventral channel.

Description

Shell (Figs 1E,F; 2B; 3C,D). Up to about 3.3 mm in length, spire outline straight to very slightly convex, aperture slightly disjunct. Protoconch (Fig 3C,D) of about 1.3 whorls, with wrinkles forming close, irregular pits (Fig 3D). Teleoconch of up to about 4 weakly convex whorls, last whorl and base evenly convex. Surface with fine orthocline growth lines and very fine spiral grooves (Fig 1E). Inner lip of aperture firmly adhering to parietal wall, outer lip weakly thickened. Colour yellow-brown, semi-translucent to opaque.

Table 4

Shell dimensions of holotype and paratypes (C.201013; n = 15; minimum, maximum, mean and standard deviation) of *Westrapyrgus slacksmithae* (in mm).

	SL	SW	AL	AW	BW	CV	TW
Holotype	2.82	1.80	1.22	0.99	2.09	0.16	3.7
Paratypes							
Min	2.54	1.60	1.15	0.89	1.91	0.120	3.3
Max	3.29	2.01	1.43	1.11	2.44	0.190	4.1
Mean	2.90	1.84	1.28	1.02	2.11	0.154	3.7
sd	0.22	0.12	0.10	0.07	0.15	0.02	0.2

Sexual dimorphism. Males (n = 11) are smaller than females (n = 4) in shell length (males 2.83 ± 0.20 mm, females 3.10 ± 0.05 mm) and width (males 1.80 ± 0.06 mm, females 1.95 ± 0.12 mm) and, although these differences for the shell width are significant (P =< 0.01) the results are inconclusive because of the small number of females measured.

Operculum (Fig 1D). With 1-5 pegs on inner surface, pegs occupying 0.14-0.48 of opercular length (mean 0.31, sd 0.090).

Table 5

Opercula measurements for paratypes (n = 15; minimum, maximum, mean and standard deviation) of *Westrapyrgus slacksmithae* (in mm).

	OL	OW	ML	PL	PH	PN
Min	0.89	0.68	0.17	0.12	0.03	1
Max	1.20	0.85	0.64	0.51	0.27	5
Mean	1.06	0.76	0.48	0.33	0.10	2.4
sd	0.11	0.06	0.12	0.10	0.08	1.45

Radula (Fig 4C). Central teeth: each with 4-5 lateral cusps, median cusp of medium width, sharply pointed, nearly twice as long as adjacent cusps; 3 pairs of basal cusps. Basal tongue U-shaped, just protruding past lateral edge. Lateral teeth: each with 4-5 cusps on both sides. Median cusp sharply pointed; less than 2 times longer than adjacent cusps. Basal projection of lateral teeth pointed. Marginal teeth: inner with 17-21 cusps; outer with 24-28 cusps.

Head-foot (Fig 5G). Cephalic tentacles with black pigment with unpigmented median dorsal stripe; snout, head and neck, foot and opercular lobe all strongly pigmentated with black or dark grey; pallial roof with mottled to uniform black pigment; visceral coil densely pigmented, mostly black or dark grey.

Anatomy (See Appendix for measurements).

Mantle Cavity. Ctenidium with 21-25 (n = 6) filaments. Osphradium elongately oval; located between posterior end and middle of ctenidium. Hypobranchial gland well developed; partly to completely covering straight to slightly arched rectum. Renal organ extends forward *ca.* ½ its length into pallial cavity; pericardium more than ½ within pallial roof.

Stomach (Fig 5D). With large caecum.

Male Reproductive System (Fig 5G). Testis of 1.3-1.5 (n = 3) whorls. Seminal vesicle tightly coiled over stomach and also coiled on both digestive gland and testis behind stomach. Prostate gland about ⅓ within pallial roof, oval in shape, broadly-oval in section. Pallial vas deferens flush with surface; strongly undulating throughout its length. Penis unpigmented, with expanded basal portion and long, evenly-tapering distal portion. Penial duct undulating in base and proximal two thirds of distal portion of penis.

Female Reproductive System (Fig 5C). Ovary of about 1.2-1.5 (n = 3) whorls. Coiled oviduct with initial U-shaped loop orientated obliquely backwards; initial loop high to medium; proximal part with bends and kinks, or twisted; with two bends distal to seminal receptacle. Coiled oviduct and bursal duct join at posterior pallial wall. Bursal duct parallel sided and straight. Oviduct joining bursal duct from right side. Seminal receptacle with short duct, ovoid in shape and located on middle of inner wall of bursa copulatrix. Rectum overlapping albumen and capsule glands. About ½ of albumen gland behind posterior pallial wall. Capsule gland with anterior end rounded, oval in section, with distinct glandular zones. Ventral channel distinct, with indistinct muscular vestibule. Genital opening small, located about ⅓ behind anterior end of capsule gland.

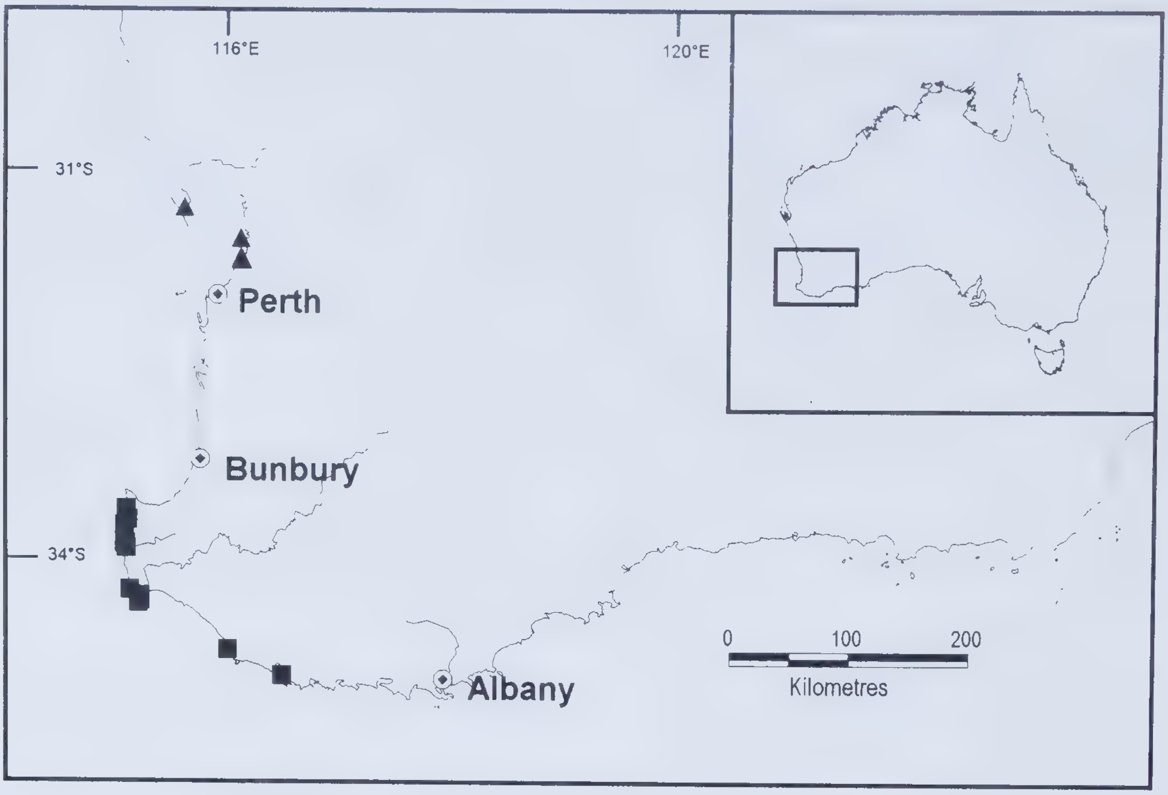

Figure 6. Map of the south west of Western Australia showing the known distribution of the two species of *Westrapyrgus westralis* n sp (■) and *Westrapyrgus slacksmithae* n sp (▲).

Etymology

Named after Mrs Shirley Slack-Smith of the West Australian Museum, who assisted in the collection of the type material.

Remarks

Kendrick (1976) in a paper detailing the degradation of the Avon River, recorded this species from that river and noted that he had first collected it in 1969. He noted that "Records are from streams in south-western Australia between the Moore and Frankland Rivers, it being found on submerged sticks, bark, stones, *etc*". This distribution conforms to the total distribution of the two taxa recorded herein. Kendrick (1976) further noted that in the Avon River "*Potamopyrgus* sp" was "known only from pools in the Walyunga National Park.... situated in the Darling Range immediately below the confluence with the comparatively fresh Wooroloo Brook". He suggested that this species might have previously occurred more widely along the Avon. Currently this species appears to be restricted to a few localities in the Avon and Moore Rivers (Kendrick 1976 and herein) and consequently its conservation status requires assessment. While it is possibly also living in other nearby drainages, with the considerable amount of collecting of macroinvertebrates in the streams along the south western seaboard it is unlikely that this reasonably conspicuous species would have been overlooked.

This species differs from *Westrapyrgus westralis* in having a more ovate shell (compare Fig 2A and B), in lacking a distinct "elbow" in the distal part of the penis, in the head-foot being heavily pigmented (almost entirely unpigmented in *W. westralis*) and in the more anterior placement of the female genital opening.

When the measured populations of the two species are compared using ANOVA, all shell measurements are significantly ($P \leq 0.001$) different. The opercular measurements are also significantly different at this level, with the exception of the length of the area occupied by the pegs and the number of pegs. Consequently the two species separate well using shell and opercular measurements with all specimens being correctly assigned in a discriminant function analysis. The two species are also readily discriminated on the basis of their radulae, particularly concerning the inner and outer marginal cusp counts. Comparisons (using t-tests) of anatomical measurements (see Appendix) show that only the length of the gastric caecum, the length of the bursa copulatrix, the width of the duct of the bursa copulatrix and the length of the capsule gland differ at the $P \leq 0.001$ level. The number of ctenidial filaments, the lengths of the renal gland and seminal receptacle and the width of the bursa copulatrix differ at the $P \leq 0.05$ level.

Discussion

Whilst some efforts have been made to sample small molluscs in fresh water systems in southern Western Australia, much remains to be done and, possibly, additional taxa will eventually be discovered. The two species described above appear to show a well-marked geographical separation. It is unclear, however, as to what extent suitable habitats (for hydrobiids) within this gap have been sampled.

The two taxa exhibit many differences in the details of the shell size and shape, as well as in details of the radula, operculum and anatomy. The recognition of a distinct genus of Hydrobiidae in southern Western Australia is not surprising given the high degree of endemism in plants and animals in that area. However, unlike many other elements of the fauna and flora in this area, *Westrapyrgus* has few distinct apomorphies separating it from its eastern relatives. It has only been possible to assign generic rank to these species after completing a detailed study of hydrobiids in other parts of Australia. This has enabled seemingly insignificant characters (such as the minute spiral grooves on the shell of both species of *Westrapyrgus*) to be used with some confidence. While it is possible to obtain useful morphological characters to separate species and genera, the very nature of these characters in this "morphostatic" radiation results in high levels of homoplasy and necessitates the use of molecular data to resolve phylogenies. The phylogenetic relationships of this group will be discussed elsewhere using such data.

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Appendix

Table of anatomical measurements of *Westrapyrgus westralis* and *W. slacksmithae*. Explanation of abbreviations used in table (in order of appearance). CTENFIL – number of ctenidial (gill) filaments; OSL – length of osphradium; CTWID – width of ctenidium; KL – length of renal gland; KW – width of renal gland; SS – length of style sac; STOML – length of stomach proper; CAEC – length of gastric caecum; PRL – length of prostate; PRW – width of prostate; PENEYE – distance between right eye and base of penis; SRL – length of seminal receptacle; SRW – width of seminal receptacle; BCL – length of bursa copulatrix; BCW – width of bursa copulatrix; BCDTW – width of bursal duct; BCDTL – length of bursal duct; AGL – length of albumen gland; AGW – width of albumen gland; CGL – length of capsule gland; CGW – width of capsule gland. Measurements in mm.

Westrapyrgus westralis n sp

	CTENFIL	OSL	CTWID	KL	KW	SS	STOML	CAEC	PRL	PRW	PENEYE	SRL	SRW	BCL	BCW	BCDTW	BCDTL	AGL	AGW	CGL	CGW
n	6	6	6	6	6	6	6	6	3	3	3	3	3	3	3	3	3	3	3	3	3
Min	19.00	0.23	0.17	0.38	0.15	0.40	0.43	0.17	0.47	0.22	0.49	0.09	0.07	0.17	0.13	0.03	0.12	0.27	0.22	0.33	0.24
Max	23.00	0.34	0.30	0.52	0.22	0.51	0.60	0.25	0.66	0.35	0.76	0.12	0.11	0.24	0.17	0.05	0.23	0.33	0.27	0.43	0.33
Mean	21.17	0.29	0.25	0.43	0.18	0.46	0.54	0.21	0.59	0.29	0.65	0.10	0.09	0.21	0.14	0.05	0.17	0.29	0.25	0.38	0.29
sd	1.47	0.04	0.05	0.06	0.02	0.04	0.06	0.03	0.10	0.07	0.14	0.02	0.02	0.03	0.03	0.01	0.05	0.03	0.03	0.05	0.05

Westrapyrgus slacksmithae n sp

	CTENFIL	OSL	CTWID	KL	KW	SS	STOML	CAEC	PRL	PRW	PENEYE	SRL	SRW	BCL	BCW	BCDTW	BCDTL	AGL	AGW	CGL	CGW
n	6	6	6	6	6	6	6	6	3	3	3	3	3	3	3	3	3	3	3	3	3
Min	21.00	0.26	0.20	0.46	0.16	0.36	0.40	0.09	0.52	0.27	0.54	0.14	0.11	0.41	0.24	0.09	0.17	0.33	0.27	0.50	0.27
Max	25.00	0.39	0.28	0.60	0.24	0.49	0.61	0.17	0.76	0.36	0.65	0.17	0.13	0.46	0.30	0.14	0.22	0.46	0.33	0.52	0.38
Mean	23.33	0.35	0.22	0.53	0.19	0.42	0.51	0.13	0.65	0.30	0.60	0.16	0.12	0.44	0.27	0.11	0.19	0.39	0.30	0.51	0.32
sd	1.51	0.05	0.04	0.06	0.03	0.05	0.07	0.03	0.12	0.05	0.05	0.02	0.01	0.03	0.03	0.03	0.02	0.07	0.03	0.01	0.06

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Records of sick, injured and dead pinnipeds in Western Australia 1980-1996

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Abstract

The management of stranded pinnipeds is often well publicized and there is strong public empathy for these animals. However, few data are available on the frequency with which sick, injured and dead pinnipeds are encountered or on the success of any applied management. This study presents what is known of stranded pinnipeds in Western Australia during the period 1980-1996. A total of 244 pinnipeds of six species were recorded sick, injured or dead during the 17 year period 1980-1996, of which 179 (73.4%) were encountered dead or died subsequently. The most commonly encountered species was *Neophoca cinerea* (110, or 61.5% of records). Of the 179 animals, 51 (28.5%) died as a result of direct or indirect interaction with humans. Twenty (39%) of the deaths caused by humans were the result of violent events directed at the pinnipeds (shot, speared, or clubbed). The species most frequently killed by human activities was *N. cinerea* (n = 47). The most common cause of unnatural death was gunshot wounds (n = 16). The most common cause of natural deaths was respiratory conditions.

Introduction

Six species of pinniped, Australian sea lion *Neophoca cinerea*, New Zealand fur seal *Arctocephalus forsteri*, subantarctic fur seal *A. tropicalis*, leopard seal *Hydrurga leptonyx*, southern elephant seal *Mirounga leonina* and crabeater seal *Lobodon carcinophagus*, have been recorded in Western Australian waters since 1980 (Table 1). The latter four species are well outside their normal Antarctic and sub-Antarctic ranges. Details of strandings of specimens of these species were subsequently archived in a Department of Conservation and Land Management (CALM) data-base. These strandings occurred on beaches along the south and lower west coast of Western Australia.

N. cinerea breeds on islands along the southern and lower western coastline of Western Australia (Gales *et al.* 1992a, 1994), while *A. forsteri* breeds on islands along the south coast of the State (Shaughnessy *et al.* 1994). The other four species of pinniped are infrequent visitors to Western Australian waters. In late 1996, two breeding records of *M. leonina* were reported (Mawson & Coughran 1999).

In Western Australia, *N. cinerea* and *A. forsteri* are afforded special protection under the provisions of the Western Australian *Wildlife Conservation Act 1950*. Neither species is considered threatened with extinction, but it is recognised that the populations of both species could decline if not afforded such protection.

Wildlife agencies have finite resources to devote to conservation of flora and fauna, but dealing with sick, injured and exhausted pinnipeds can require considerable effort and resources. Continued expenditure of resources is likely to be influenced by what has been learnt from past experiences and the likelihood of favourable outcomes from attending to sick and injured animals. This paper summarizes what has been learnt from dealing with these six species of pinniped over the period 1980-96.

Methods

Records of pinnipeds were kept during the period 1 January 1980 to 31 December 1996. Reports of pinnipeds on the Western Australian coast are routinely made to the Western Australian Department of Conservation and Land Management (CALM) and are investigated if they are unusual or to determine if intervention appears necessary. CALM staff attended strandings either to investigate the deaths of animals or to assess the animals to determine what action, if any, was required. In a small number of cases information was obtained from other government officers (*e.g.* Fisheries Officers), or from members of the public. Information presented here has been used in the development of the draft *Western Australian Pinniped Management Program 1999-2008* (Gales & Wyre 1999) and the draft *Western Australian Protocols for Handling and Treatment of Sick, Injured, Incapacitated, Transient or Dead Pinnipeds* (Gales 1999). It was also used in the preparation of the *Wildlife Conservation (Close Season for Marine Mammals) Notice 1998* (Western Australian Govt Gazette, 18/9/98 pp 5155-5157).

Details relating to each case [species, location, sex, body measurements (where possible), cause of death] were recorded in a data-base maintained by CALM. No

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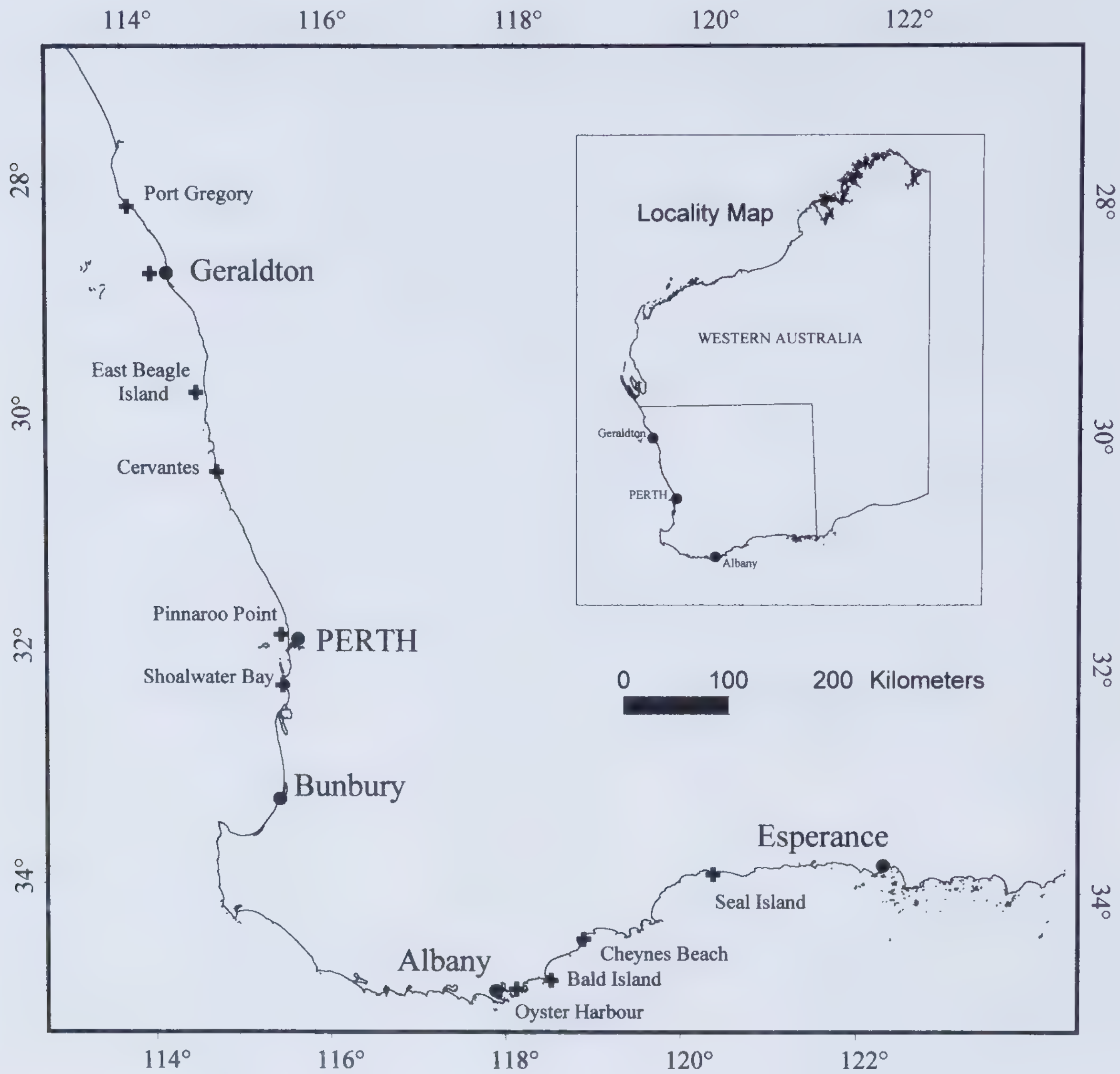

Figure 1. Map of southwest Western Australia showing the location of sites where pinnipeds have died violent deaths due to direct contact with humans (● Major towns, ✚ locations where animals were shot).

records were accepted unless the identification of the animal was verified by the data-base custodian (DKC). The data presented here do not include records of healthy animals that hauled out on beaches, and required no assistance or intervention.

Post mortems to determine the cause of death were conducted whenever possible, dependant upon access to Agriculture Western Australia veterinary staff. Many pinnipeds were too badly decomposed for post mortems. As a result of the identification of *Mycobacterium tuberculosis* in *A. forsteri* and *N. cinerea*, CALM staff now wear full protective clothing, including gloves and face mask, when handling these species.

Management of live pinnipeds in the context of this paper covered a wide range of actions, from simply excluding the public from disturbing an animal while it recuperated on a beach, through to capture and relocation to an intensive rehabilitation facility. Management of dead animals ranged from leaving the carcase *in situ* and recording relevant details, through to removal of the animal for post mortem examination and disposal or lodging it in the Western Australian Museum.

The data presented here include the records of 17 *A. tropicalis* reported by Gales *et al.* (1992b) from Western Australia (prior to 1986, *A. tropicalis* was not recognised as occurring in Western Australian waters). The data do not include those pinnipeds that died as a result of oil contamination following the sinking of the bulk ore carrier *Sanko Harvest* off the southern coast of Western Australia in February 1991. For details of that incident see Gales (1991).

Results

During the 17 years of this study, a total of 244 stranded pinnipeds were recorded, the bulk of which were *N. cinerea* (n = 150). The reporting rate varied between years and was influenced by changes in field staff, increasing knowledge and experience in species identification and a change from a centralised to a regional reporting system within CALM. Consequently these data should not be taken to indicate any trends in encounter rates. Full details relating to the four species considered infrequent visitors to coastal waters are given in Appendix 1.

Species accounts

Australian sea lion *Neophoca cinerea*. A total of 150 sea lions (61.5% of all records) were recorded on the database (Table 1), of which 14.0% returned to the wild, 83.3% were either recovered dead or died while receiving treatment, and 2.7% for which the fate was not recorded. In the 16 years in which *N. cinerea* were encountered (no animals in 1982), 75.6% were recovered dead or subsequently died. Of the 59 *N. cinerea* for which cause of death was known, 47 (or 79.7%) died due to human interference (Tables 2, 3). Examination of the sex ratio for *N. cinerea* encountered indicates an apparent bias towards large males (81 male, 29 female, 41 unknown).

New Zealand fur-seal *Arctocephalus forsteri*. Eleven *A. forsteri* (4.5% of the total records), were recorded (Table 1), of which 27.3% returned to the wild and 72.7% were either recovered dead or died while receiving treatment. 73.7% of the fur-seals were recovered dead or died subsequently each year. Of the three *A. forsteri* for which the cause of death was known (one animal was euthanased due to old age and poor condition) two died due to tuberculosis infections, while none died due to human interference (Tables 2, 3).

Subantarctic fur-seal *Arctocephalus tropicalis*. Forty-five *A. tropicalis* (18.4% of the total records) were recorded, all since 1986 (Table 1). Of these, 37.7% returned to the wild and 62.2% were either recovered dead or died while receiving treatment. 67.1% of the fur-seals were recovered dead or died subsequently in each year. Of the seven *A. tropicalis* for which the cause of death was known, two died due to human interference (Tables 2, 3).

Leopard seal *Hydrurga leptonyx*. Twenty-seven *H. leptonyx* (11.1% of the total records) were recorded, all since 1986 (Table 1), of which 44.4% returned to the wild and 55.6% were either recovered dead or died while receiving treatment. 62.6% of the leopard seals were recovered dead or subsequently died in each year. Of the three *H. leptonyx* for which the cause of death was known, two died due to human interference (Tables 2, 3).

Southern elephant seal *Mirounga leonina*. Eight *M. leonina* (3.3% of total records) were recorded, all since 1990 (Table 1), of which 87.5% returned to the wild and 12.5% were either recovered dead or died while under observation. In the four individual years in which *M. leonina* were encountered, none of the seals required veterinary intervention and none died due to human interference (Tables 2, 3). The one death recorded was that of a newborn pup (see Mawson & Coughran 1999).

Crabeater seal *Lobodon carcinophagus*. Three *L. carcinopahgus* (1.2% of the total records) were recorded, all since 1982 (Table 1), of which 33.3% returned to the wild and 66.7% were either recovered dead or died while receiving treatment. In the two individual years in which *L. carcinophagus* were encountered, 75.0% of the seals were recovered dead or subsequently died. None of the deaths could be attributed to human interference. The cause of death for one animal was known (Table 3) and the other animal died in captivity while receiving treatment, but the precise cause of death was not determined.

In summary, a total of 179 animals (73.4% of the total records) were encountered dead, or subsequently died. Of those 179 animals, 51 (28.5%) were found to have died as a direct or indirect result of interaction with humans.

Table 1

Numbers of each species of pinniped encountered by CALM staff 1980-1996 in Western Australia. Values in parentheses indicate the number of seals returned to wild, the number which died, and the number for which fate is unknown).

Year	*Neophoca cinerea*	*Arctocephalus forsteri*	*Arctocephalus tropicalis*	*Hydrurga leptonyx*	*Mirounga leonina*	*Lobodon carcinophagus*	Total
1980	8 (1,6,1)	1 (0,1,0)	0	0	0	0	9 (1,7,1)
1981	1 (1,0,0)	0	0	0	0	0	1 (1,0,0)
1982	0	0	0	0	0	1 (0,1,0)	1 (0,1,0)
1983	3 (1,2,0)	0	0	0	0	0	3 (1,2,0)
1984	2 (0,2,0)	0	0	0	0	0	2 (0,2,0)
1985	5 (2,3,0)	0	0	0	0	0	5 (2,3,0)
1986	8 (6,2,0)	0	1 (1,0,0)	6 (1,5,0)	0	0	15 (8,7,0)
1987	6 (2,4,0)	0	3 (1,2,0)	1 (0,1,0)	0	0	10 (3,7,0)
1988	19 (2,17,0)	1 (0,1,0)	4 (1,3,0)	1 (1,0,0)	0	0	25 (4,21,0)
1989	23 (3,20,0)	0	3 (1,2,0)	0	0	0	26 (4,22,0)
1990	19 (0,19,0)	3 (1,2,0)	1 (0,1,0)	8 (6,2,0)	1 (1,0,0)	0	32 (8,24,0)
1991	14 (1,12,1)	0	1 (0,1,0)	0	1 (1,0,0)	0	16 (2,13,1)
1992	8 (0,8,0)	2 (1,1,0)	11 (1,10,0)	5 (2,3,0)	0	0	26 (4,22,0)
1993	14 (2,11,1)	2 (0,2,0)	6 (4, 2,0)	1 (0,1,0)	0	2 (1,1,0)	25 (7,17,1)
1994	6 (0,5,1)	1 (1,0,0)	6 (3,3,0)	0	0	0	13 (4,8,1)
1995	8 (0,8,0)	1 (0,1,0)	4 (2,2,0)	2 (0,2,0)	1 (1,0,0)	0	16 (3,13,0)
1996	6 (0,6,0)	0	5 (3,2,0)	3 (2,1,0)	5 (4,1,0)	0	19 (9,10,0)
Total	150 (21,125,4)	11 (3,8,0)	45 (17,28,0)	27 (12,15,0)	8 (7,1,0)	3 (1,2,0)	244 (61,179,4)

Table 2

Causes of death of pinnipeds in Western Australia involving human influences. (n = 47 *N.cinerea*, n = 2 *A. tropicalis*[a] and n = 2 *H. leptonyx*[b], one in each year for both *A. tropicalis* and *H. leptonyx*).

Cause	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	Total
Shot	7	0	0	1	1	0	2^b	1	0	1	1	1	0	1	0	0	0	16
Boat Propeller	0	0	0	0	1	1	0	0	2	0	1	1	0	1	0	0	1	8
Lobster Pots/lines	0	0	0	0	0	0	1	0	1	2	1	0	2	0	0	0	0	7
Fishing lines/hooks	2	0	0	0	0	0	2^b	0	0	0	0	0	0	3	0	0	0	7
Fishing nets	0	0	0	0	0	0	0	0	3	1	0	0	1^a	2^a	0	0	0	7
Speared	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	3
Plastic bands	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Clubbed	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Total	10	0	0	2	2	1	6	1	7	4	3	2	3	8	1	0	1	51

Table 3

Natural causes of death (where known) of pinnipeds in Western Australia.

Cause	*N. cinerea*	*A. forsteri*	*A. tropicalis*	*H. leptonyx*	*L. carcinophagus*	Total
Pneumonia	3	0	1	0	0	4
Pleurisy	2	0	0	0	0	2
Bronchitis	1	0	0	0	0	1
Mycobacterium tuberculosis	2	2	0	0	0	4
Histiocytic tumor	2	0	0	0	0	2
Septicaemia	1	0	0	0	0	1
Toxaemia	0	0	0	0	1	1
Gastro-enteritis	0	0	1	0	0	1
Cestodes/nematodes	0	0	3	0	0	3
Abscess	1	0	0	0	0	1
Immune system failure	0	0	0	1	0	1
Total	12	2	5	1	1	21

Unnatural causes of death

The causes of death could be grouped into eight categories for unnatural deaths (Table 2) and 11 categories for natural deaths (Table 3). The species most frequently affected by human activities was *N. cinerea* (n = 47, 65.3% of deaths for which cause was determined); in addition there were two records each for *A. tropicalis* and *H. leptonyx*. The most common cause of unnatural death was shooting (n = 16, 31.4% of the unnatural deaths), including a shooting of six animals on one occasion in 1980.

The next most common causes of death in decreasing order of occurrence were; boat collisions (n = 8, 15.7%), juvenile animals drowning in lobster pots or attached ropes (n = 7, 13.7%), entanglement in fishing line/hooks (n = 7, 13.7%), drowning in fish nets (n = 7, 13.7%), speared or shot with arrows (n = 3, 5.9%), choked by plastic bait bands/straps (n = 2, 3.9%), and clubbed to death (n = 1, 1.9%).

For the 16 animals which were shot (15 *N. cinerea*, 1 *H. leptonyx*), all shootings were likely to have occurred in areas with either active fishing fleets or major human populations (Fig 1); note that the site of shooting might not necessarily be the same as the location where the injured/dead animal comes ashore. Ten seals were shot in the Albany area (6 recovered at Bald Island, 2 at Oyster Harbour, 1 at Cheynes Beach, and 1 at Seal Island near Hopetoun). Four animals were shot along the mid-west coast area from Port Gregory south to Cervantes (1 recovered at Port Gregory, 1 at Geraldton, 1 at East Beagle Island, and 1 at Cervantes). Two shootings occurred along the Perth metropolitan coast (1 animal recovered at Pinnaroo Point, and 1 at Shoalwater Bay). The shooting at Pinnaroo Point, near Yanchep, involved the *H. leptonyx*, and one *N. cinerea* was killed with an arrow at Shoalwater Bay (included in the 'Speared' category in Table 2).

Natural causes of death

Post mortems identified the principal cause of death in 21 cases (12 *N. cinerea*, 2 *A. forsteri*, 5 *A. tropicalis*, 1 *H. leptonyx* and 1 *L. carcinophagus*). A wide range of causes was identified (Table 3), with respiratory conditions being the most common group. Four cases of tuberculosis (*Mycobacterium tuberculosis*) were recorded, with two records each from *N. cinerea* and *A. forsteri* (Cousins *et al.* 1993).

Discussion

The data presented here indicate that a high percentage (51 of 179, or 28.5%) of the pinnipeds found dead or moribund on Western Australian beaches have been adversely affected by humans in some way. Thirty-nine percent (20 of 51) of animals that died from interactions with humans, suffered violent deaths (16 shot, 3 speared and 1 clubbed) and a further 16% died as a result of injuries sustained from collisions with small boats (total 55%). These figures are likely to be underestimates, given that many carcases were too decomposed to determine the cause of death.

The number of animals that die from collisions with boats can be expected to increase as recreational boating activity increases along the west and south coast of Western Australia, particularly where such activities occur in close proximity to haul-out sites or breeding islands. If the populations of sea lions and fur seals continues to increase, then the numbers killed in collisions with boats is also likely to increase. There is scope for public education programs to advise boat owners how to interact with pinnipeds. There may also be a need to legislate to restrict the close approach of small boats to haul-out sites and breeding colonies. The development of standard guide-lines similar to those adopted for interactions with cetaceans should enable humans to interact with pinnipeds without having an adverse impact on their populations.

The estimated population of *N. cinerea* in Western Australia is 2600-3400 (Gales *et al.* 1994) while that of *A. forsteri* is 7000 (Shaughnessy *et al.* 1994). Despite the greater numbers of *A. forsteri* along the Western Australian coastline, *N. cinerea* suffered more from adverse interactions with humans. The population of *N. cinerea* along the west coast is slightly smaller than that occurring along the south coast but suffered a greater number of deaths. This was most probably due to the fact that prime sea lion habitat on the west coast occurs closer to the main human population centres where boating and fishing activities are more common. Male *N. cinerea* were encountered nearly three times as often as females, and males died violent deaths twice as often as females. This is most likely a reflection of the dispersal and foraging behaviour of males and proximity of several major haul-out sites close to large cities and towns and to commercial fishing zones (Gales *et al.* 1992a). Females are rarely seen at these sites.

Success in reducing the incidence of violent death amongst pinnipeds will depend partly on the co-operation of the public in reporting these illegal activities, the judicial system applying appropriate penalties, and on education programs to raise public awareness of how to report stranded animals and to safely interact with pinnipeds.

Thirty-five of 41 (85%) *A. tropicalis* encountered were significantly underweight. This suggests that these animals were not foraging successfully and these records may represent extra-limital movements.

Eight *H. leptonyx* died while in care, several while under anaesthesia, four were euthanased due to their poor condition, and only one was released back to the wild. This species is large, strong and can be particularly aggressive even when ill. Given the difficulties encountered so far in treating this species, continued capture and attempts at rehabilitation seem unwise.

The establishment and maintenance of a data-base such as the one used by CALM provides a valuable means of storing data on species of pinniped which seldom visit mainland Australia (*e.g. H. leptonyx, M. leonina,* and *L. carcinophagus*). Post mortem examinations and pathology also give an insight into the natural diseases from which these species suffer. Such information can be important in interpreting significant or sudden changes in wild populations.

Recent events elsewhere in Australia have shown that diseases in native wildlife can have significant implications for their management *e.g.* morbillivirus in pinnipeds (Mahy *et al.* 1988) and cetaceans, lyssavirus in megachiropterans, and viral chorio-retinitis in large *Macropus* sp. The discovery of diseases such as *M. tuberculosis* in pinnipeds also has significant occupational welfare implications for those people handling infected animals (live or dead).

The question of value-for-money in dealing with pinniped strandings is difficult to resolve. It is fairly easy to quantify the cost of managing sick or injured pinnipeds (veterinary costs, post mortems, carcase disposal, travel expenses), but it is difficult to determine the value of the information gained, particularly from species rarely encountered in Australian waters which might not otherwise be studied. Neither is it easy to quantify the value of the positive public relations which can be obtained through caring for (and in some cases releasing) pinnipeds. Public perception of Australian native fauna is largely limited to a few well-known terrestrial species (*e.g.* kangaroos and koalas). In a State with such a large coastline and many population centres located along the coastline, limited active management and passive data collection provides an opportunity to raise public awareness of conservation issues associated with a little appreciated group of our native fauna.

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Appendix 1

Summary of accounts for individual animals for the four species of non-resident pinnipeds encountered in Western Australia 1980-96. Note: data for *A. tropicalis* follow on from those presented by Gales *et al.* (1992b).

	Date	Sighting/Collection Site	Sex	History
Leopard seal *Hydrurga leptonyx*				
1	14/10/83	Peppermint Beach 33°32'S, 115°29'E	?	Returned to the sea.
2	27/07/86	Pinnaroo Point 31°49'S, 115°44'E	M	Head wound caused by gun shot, died in captivity.
3	1/09/86	Bunbury 33°19'S, 115°38'E	?	Wounds to mouth and underside, died in captivity.
4	6/09/86	Geographe Bay 33°37'S, 115°08'E	?	Poor condition, lacerations to throat and flippers from shark attack, died in captivity after some years.
5	17/10/86	Denmark 34°57'S, 117°21'E	?	Died in captivity.
6	17/11/86	Florida Beach 32°38'S, 115°37'E	M	Poor condition, internal injury caused by fishing hooks, died in captivity.
7	24/10/87	Smiths Beach 33°39'S, 115°02'E	F	Deep wounds to head and neck, bone infection. Euthanased.
8	10/09/88	Two Rocks 31°30'S, 115°35'E	F	Dehydrated, poor body condition. Rehabilitated and released 4/11/88.
9	16/06/90	Cape Le Grand 34°01'S, 122°07'E	?	Rested before returning to sea.
10	27/08/90	Denmark 34°55'S, 117°32'E	?	Rested before returning to sea.
11	1/09/90	Salmon Holes, Tornidirrup 35°07'S, 117°55'E	?	Found dead.
12	1/09/90	Salmon Holes, Tornidirrup 35°07'S, 117°55'E	?	Swimming off shore.
13	8/09/90	Lancelin 31°01'S, 115°20'E	?	Rested before returning to sea.
14	11/09/90	Four Mile Beach, Esperance 33°52'S, 121°53'E	?	Wounds from shark attack, recovered after resting and returned to sea.
15	2/10/90	Walpole 34°59'S, 116°44'E	?	Found dead.
16	11/10/90	Free Beach 33°51'S, 121°55'E	?	Wound to head – returned to the sea.
17	21/08/92	Seabird 31°16'S, 115°26'E	?	Hauled out to rest but returned to the sea after harassment by people.
18	22/08/92	Esperance 33°52'S, 121°53'E	F	Hauled out, infected left eye – bite injury. Died under anaesthetic.
19	25/08/92	San Remo 32°29'S, 115°45'E	?	Found dead.
20	17/09/92	Cowaramup (Gracetown) 33°52'S, 114°58'E	?	Found exhausted, rested then returned to sea.
21	6/11/92	Thirsty Point – Cervantes 30°30'S, 115°04'E	M	Weak and emaciated, died 7/11/92.
22	22/10/93	Geraldton 28°46'S, 114°37'E	M	Poor body condition, weak and lethargic. Euthanased.
23	1/09/95	Princess Royal Harbour, Albany 35°04'S, 117°53'E	F	Found in poor condition, severely emaciated, laboured breathing. Euthanased.
24	4/09/95	Mutton Bird Beach, Torbay 35°04'S, 117°44'E	M	Found in an emaciated state and non-responsive. Euthanased.
25	4/08/96	Two Peoples Bay 34°57'S, 118°11'E	?	Rested on beach till 5/8/96, then returned to sea.

Appendix 1 (continued)

	Date	Sighting/Collection Site	Sex	History
26	13/08/96	Cottesloe 31°59′S, 115°45′E	M	Died 7/09/96 while receiving intensive treatment.
27	12/09/96	Ten Mile Beach, Esperance 33°51′S, 121°55′E	M	Rested on beach, returned to sea 15/09/96.
Elephant seal ***Mirounga leonina***				
1	10/07/90	Cheynes Beach 34°34′S, 118°45′E	F	Rested in the area for 3 weeks then returned to sea.
2	12/02/91	Fremantle 32°03′S, 115°45′E.	F	Several wounds. Released off Port Beach.
3	19/01/95	Tulki, Ningaloo Marine Park 22°02′S, 113°54′E	M	Hauled out at Tulki, west of Exmouth. No action required.
4	15/10/96	Wylie Bay 33°52′S, 121°53′E	F + pup	Live birth, pup died soon after birth. Lodged in WA Museum. (WAM #M48667)
5	12/11/96	Epineux Bay 26°20′S, 113°18′E	F + pup	Live birth, both animals went to sea.
6	23/12/96	Windy Harbour 34°50′S, 116°01′E	F	Good condition, went to sea soon after.
Crab-eater seal ***Lobodon carcinophagus***				
1	17/07/82	Safety Bay 32°19′S, 115°44′E	F	Found alive, died in captivity.
2	7/01/93	Mandurah 32°32′S, 115°43′E	F	Good condition, taken by sea to a beach on the west side of Garden Island, found dead on 10/1/93.
3	3/02/93	Princess Royal Harbour 35°04′S, 117°53′E	?	Rested, then went to sea.
Subantarctic fur seal ***Arctocephalus tropicalis***				
1	20/09/86	Kalbarri 27°43′S, 114°10′E	F	Found alive on beach. Kept at Atlantis, later transferred to Taronga Zoo.
2	1/09/87	Gordon Inlet 34°17′S, 119°28′E	M	Found alive on beach. Very underweight. Died 2/09/87, lodged at WA Museum. (WAM #M27189)
3	8/09/87	Point Anne 34°11′S, 119°35′E	F	Found dead on beach. Lodged at WA Museum. (WAM #M27192)
4	27/09/87	Two Rocks 31°30′S, 115°35′E	M	Found alive on beach. Underweight. Taken into care, released 7/12/90.
5	27/07/88	Sea Bird 31°16′S, 115°26′E	F	Found alive on beach. Underweight. Died 28/07/88.
6	12/09/88	Canal Rocks 33°41′S, 114°59′E	?	Found alive on beach. Underweight. Died on beach.
7	9/10/88	Yokinup Bay 33°52′S, 123°02′E	M	Found alive on beach. Underweight. Taken into care, released 7/12/90.
8	29/10/88	Nanarup Beach 35°00′S, 118°04′E	F	Found alive on beach. Underweight. Died 1/11/88.
9	10/01/89	Two Peoples Bay 34°57′S, 118°11′E	M	Found alive on beach. Underweight. Taken into care, released 7/12/90.
10	2/10/89	Cheynes Beach 34°34′S, 118°45′E	F	Found emaciated, dead.
11	5/10/89	Cottesloe 31°59′S, 115°45′E	?	Found dead.
12	12/11/90	Quaggi Beach 33°49′S, 121°10′E	?	Emaciated, died 13/11/90.
13	6/09/91	Eagle Bay 33°33′S, 115°04′E	F	Found alive. Euthanased.
14	14/08/92	Avalon Beach 32°34′S, 115°39′E	F	Found dead. Fishing net entanglement.
15	22/08/92	Frenchman's Bay, Albany 35°02′S, 117°53′E	M	Found emaciated, dead.
16	24/08/92	Frenchman's Bay, Albany 35°04′S, 117°53′E	?	Found emaciated, dead.
17	29/08/92	Preston Beach 32°54′, 115°39′E	M	Blind in left eye, emaciated, severe pneumonia. Euthanased.
18	11/09/92	Peaceful Bay 35°02′S, 117°53′E	?	Found in emaciated condition 8/9/92. Euthanased. Fish bone in oesophagus.
19	19/09/92	Cottesloe 31°59′S, 115°45′E	M	Found emaciated, dead.
20	22/09/92	Albany 35°02′S, 117°53′E	?	Found dead.
21	7/10/92	Princess Royal Harbour 35°04′S, 117°53′E	F	Found emaciated, dead.

Appendix 1 (continued)

	Date	Sighting/Collection Site	Sex	History
22	9/11/92	Peaceful Bay 35°02′S, 117°53′E	M	Found alive in poor condition. Euthanased. Fish bone lodged in diaphram, roundworm infection.
23	14/12/92	Trigg Beach 31°52′S, 115°45′E	M	Transported to Augusta and released.
24	22/12/92	Princess Royal Harbour 35°04′S, 117°53′E	?	Found alive, emaciated. Euthanased.
25	24/01/93	Yanchep 31°33′S, 115°37′E	M	Picked up in a weak condition. Treated until 12/2/93, released off Augusta.
26	14/04/93	Green Pool, Denmark 34°57′S, 117°21′E	?	Engangled in fishing net, but found alive. Treated and released.
27	9/05/93	Esperance 33°51′S, 121°55′E	F	Found alive and emaciated, severe worm infection. Euthanased.
28	2/07/93	Hillarys Marina, Sorrento 31°50′S, 115°45′E	M	Poor condition, rehabilitated and released.
29	21/07/93	Wylie Bay 33°50′S, 122°00′E	M	Found alive, emaciated but died.
30	19/10/93	North West Cape, Jantz Access 21°47′S, 114°10′E	?	Resting on beach, returned to sea.
31	5/08/94	Injidup Beach 32°42′S, 114°59′E	F	Found alive, emaciated. Died later.
32	14/08/94	Swanbourne 31°58′S, 115°46′E	M	Emaciated and weak. Rehabilitated and released off Cape Leeuwin.
33	28/08/94	Preston Beach 32°54′S, 115°39′E	M	Emaciated and weak, died 29/08/94.
34	21/09/94	Two Rocks 31°30′S, 115°35′E	F	Rested then returned to sea.
35	22/09/94	Golden Bay 32°29′S, 115°45′E	F	Found emaciated, dead.
36	29/11/94	Geraldton 28°46′S, 114°37′E	?	Hauled out, poor condition. Rehabilitated then released.
37	21/07/95	Point Peron 32°16′S, 115°41′E	M	Hauled out, poor condition. Rehabilitated then released.
38	11/08/95	Green Head 30°04′S, 114°58′E	M	Emaciated and weak, died overnight.
39	15/08/95	Cervantes 30°30′S, 115°04′E	M	Emaciated and weak, died overnight.
40	8/10/95	Port Geographe, Busselton 33°39′S, 115°20′E	M	Weak and emaciated, rehabilitated and released off Hamelin Bay.
41	4/08/96	Mullaloo Beach 31°47′S, 115°44′E	M	Found weak and emaciated. Died in captivity.

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Obituary: Graeme Talbot Smith (February 1938 – June 1999)

GRAEME TALBOT SMITH was born in Adelaide on the 10th of February 1938 and died on the 30th of June in Perth, aged 61. Ironically, he was informed that he had pancreatic cancer on his 61st birthday. From his diagnosis to his untimely death, Graeme fought a tough, but unwinable, battle against the cancer. What struck all those who saw him during this period was his calm acceptance of his terminal condition and the equanimity he displayed throughout his illness.

After school in Melbourne, Graeme majored in Zoology and Geology at Melbourne University, working in Kalgoorlie during one of his university breaks. His first published paper was a note on a bat mandible found in a cave in Victoria [1964 Vic. Nat. 81: 78-79]. In 1964 he studied the ecology of *Urodacus abruptus*, a species of scorpion, for his Honours in Zoology at the Australian National University (ANU) in Canberra. His second scientific paper was on *Urodacus abruptus* [1966 Australian Journal of Zoology 14: 383-398]. This started a love of scorpions that continued throughout his working life and much of his spare time. Wherever he went he collected scorpions, measured burrows and went on night expeditions with an ultraviolet light to census scorpions. They fluoresce under UV light as his wife Helen well remembers, having chased escaped members of the captive colony he kept at home. Graeme delighted in taking people on his scorpion hunting expeditions, waxing lyrical on the wonders of the world of scorpions. He was planning to write a book on scorpions, however, he ran out of time.

In 1965, Graeme joined the Australian National Antarctic Research Expedition and spent 2 seasons (1966 and 1967) on Macquarie Island where he worked on the Royal Penguin *Eudyptes chrysolophus*, studying for a PhD at ANU [1970 Studies on the behaviour and reproduction of the Royal Penguin *Eudyptes chrysolophus schlegeli*. PhD thesis Australian National University].

Graeme was appointed to CSIRO Division of Wildlife Research in Western Australia in February 1970 to work on the Noisy Scrub-bird *Atrichornis clamosus* [1981 Biol. Conserv. 19: 239-254]. This research formed the basis of much of the Department of Conservation and Land Management's successful recovery program for this species [1996 Wildlife Management Program 12, Department of Conservation and Land Management]. During this period he also worked on the endangered Western Whipbird *Psophodes nigrogularis* and Western Bristlebird *Dasyornis longirostris* [1985 in J Ford's edited volume on Fire Ecology and Management in Western Australian Ecosystems, pp 95-102]. He then worked on corellas as part of a research group studying the ecology of cockatoos with Ian Rowley and Denis Saunders [1982 Aust. Wildl. Res. 9: 541-556; 1986 Aust. Wildl. Res. 13: 275-85; 1991 Wildl. Res. 18: 91-110; 1992 Emu 92: 19-27], then on small animals in the Kellerberrin area, forming a productive relationship with Max Abensperg-Traun [1996 Journal of Applied Ecology 33: 1302-1310].

A superb natural historian and an enthusiastic teacher, Graeme was very well read and knowledgeable on a wide range of subjects. The following story illustrates this point. One morning while on holiday on Rottnest Island, Graeme and DAS were scanning birds on Government House Lake. DAS saw 2 birds among a raft of banded stilts and asked Graeme "what are those 2 birds, with the pointed bills, spinning around like tops among the banded stilts?" Graeme looked at them and said "they're phalaropes if ever I saw them." DAS said "have you ever seen any?" and he replied "no, but that's what they would be if ever I saw them." He then described the characteristics of phalaropes from memory of something he had been reading. This incident resulted in a paper by Graeme on the red-necked phalarope in southwestern WA [1980 West. Aust. Nat. 14: 237-8.]

Graeme retired from CSIRO on the 9th of February 1993, but continued as an active Research Fellow and member of the Western Australian CSIRO research group until shortly before his death. In this capacity he worked with Terri Lloyd and the Dongerlocking Landcare Group near Dumbleyung. His last published paper was on the ecology of a scorpion *Urodacus armatus* [1998 Pacific Conservation Biology 4: 209-214]; this was his seventy-sixth publication.

Graeme is survived by his wife Helen and his daughters Katy and Lizzie. He will also be missed by his many friends and colleagues who enjoyed his breadth of knowledge, his cheerfulness and his generosity in helping others.

Denis A Saunders & Ian Rowley

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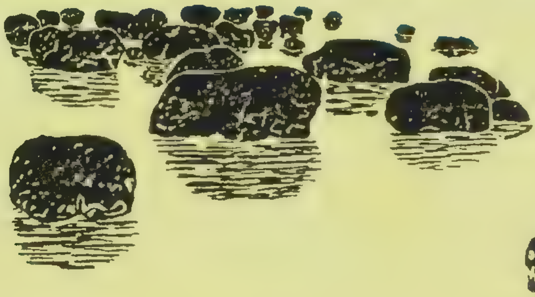

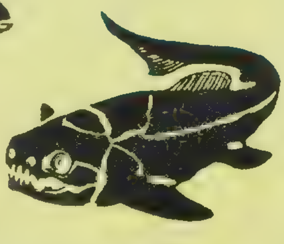

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The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor) and the Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Escape of cultured barramundi (*Lates calcarifer* Bloch) into impoundments of the Ord River system, Western Australia

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Abstract

Mitochondrial DNA sequences were used to compare barramundi found in impounded parts of the Ord River system to their cultured counterparts from a fish farm in one dam (Lake Argyle). Two haplotypes were common to all fish sampled, indicating the high probability that farmed fish are escaping, and could potentially interact with the wild population of the lower Ord River. Although the Lake Argyle barramundi farm currently produces only about 50 tonnes of fish per year, there are plans to expand barramundi production at Lake Argyle by up to 200 times this amount. If that was to occur and no efforts were made to reduce the escape of cultured fish, then sufficient numbers of escaped barramundi may survive to reproduce in the wild fishery. Maintaining the genetic integrity of wild barramundi populations will be best achieved by setting and enforcing standards to minimise escapes from fish farms.

Introduction

Fish are among the world's most intensively cultured organisms. Many species are being propagated for both restocking programs and as founders of novel cultured populations elsewhere, and large numbers of farmed fish are also escaping unintentionally from aquaculture facilities (Bergen *et al.* 1991; Lund *et al.* 1991; Gausen & Moen 1991; Webb *et al.* 1993; Windsor & Hutchinson 1995). A significant frequency and scale of escape of farmed fish has been described by Webb *et al.* (1991) as "inevitable", with numbers of escaped salmonids approaching or exceeding the numbers of naturally produced fish in certain places (Saunders 1991). Thus, the global expansion of fish farming has implications for both cultured and natural fish populations (Fleming & Gross 1993; Hayes *et al.* 1996).

Captive rearing conditions combined with artificial selection, intentional or not, cause fish to diverge from their wild phenotype through environmental and genetic processes (Cross & Challanain 1991; Swain *et al.* 1991). Further, the small numbers of broodstock typically used in fish culture encourage genetic divergence through inbreeding (Tave 1993). There is evidence that fish derived from cultured populations may have both ecological (*e.g.* competition, disease introductions) and genetic (*e.g.* loss of genetic adaptation, genetic homogenization) impacts on wild populations (*e.g.* Rinne & Minckley 1985; Loudenslager *et al.* 1986; Ferguson 1990; Bartley & Gall 1991; Hindar *et al.* 1991; Waples 1991; Wilde & Echelle 1992; Heggberget *et al.* 1993; Fleming *et al.* 1996; Einum & Fleming 1997). There remain, however, few data on exactly how cultured and wild fish interact, and these mostly concern salmonids in the northern hemisphere (Fleming & Gross 1993; Fleming *et al.* 1996; Einum & Fleming 1997).

Barramundi (*Lates calcarifer* Bloch) is a highly fecund and euryhaline fish with a tropical Indo-West Pacific distribution including northern Australia. There are around 30 commercial barramundi farms in Australia, producing approximately 500 tonnes in 1996 (Brown *et al.* 1997). Both the progeny for grow-out operations and the broodstock themselves are typically descendants of those broodstock used to begin the industry in government facilities in Queensland and the Northern Territory some years ago. Therefore, comparatively few broodstock may have founded much of the present barramundi culture industry in Australia. For example, in its few years of operation, the aquaculture facility at Lake Argyle in Western Australia (Fig 1) has reared the progeny of broodstock supplied by the government hatchery in the Northern Territory. No more than four broodstock captured from the coast near Darwin have been used in group larval production for the Lake Argyle farm, with one highly fecund female producing about 75% of all progeny so far supplied (G Schipp, Hatchery Manager, Aquaculture Branch, Department of Primary Industry and Fisheries, Northern Territory, pers comm).

In recent years, there has been an increasing incidence of barramundi caught as a bycatch of the Lake Argyle catfish (*Arius* spp) fishery, and by recreational fishers in Spillway Creek, to which waters from Lake Argyle flow when the lake exceeds the bank-full stage. Spillway Creek joins a natural watercourse (Stonewall Creek) some distance downstream, and then the Lake Kununurra irrigation diversion dam (*i.e.* the Ord River; Fig 1). At least two explanations can account for the presence of

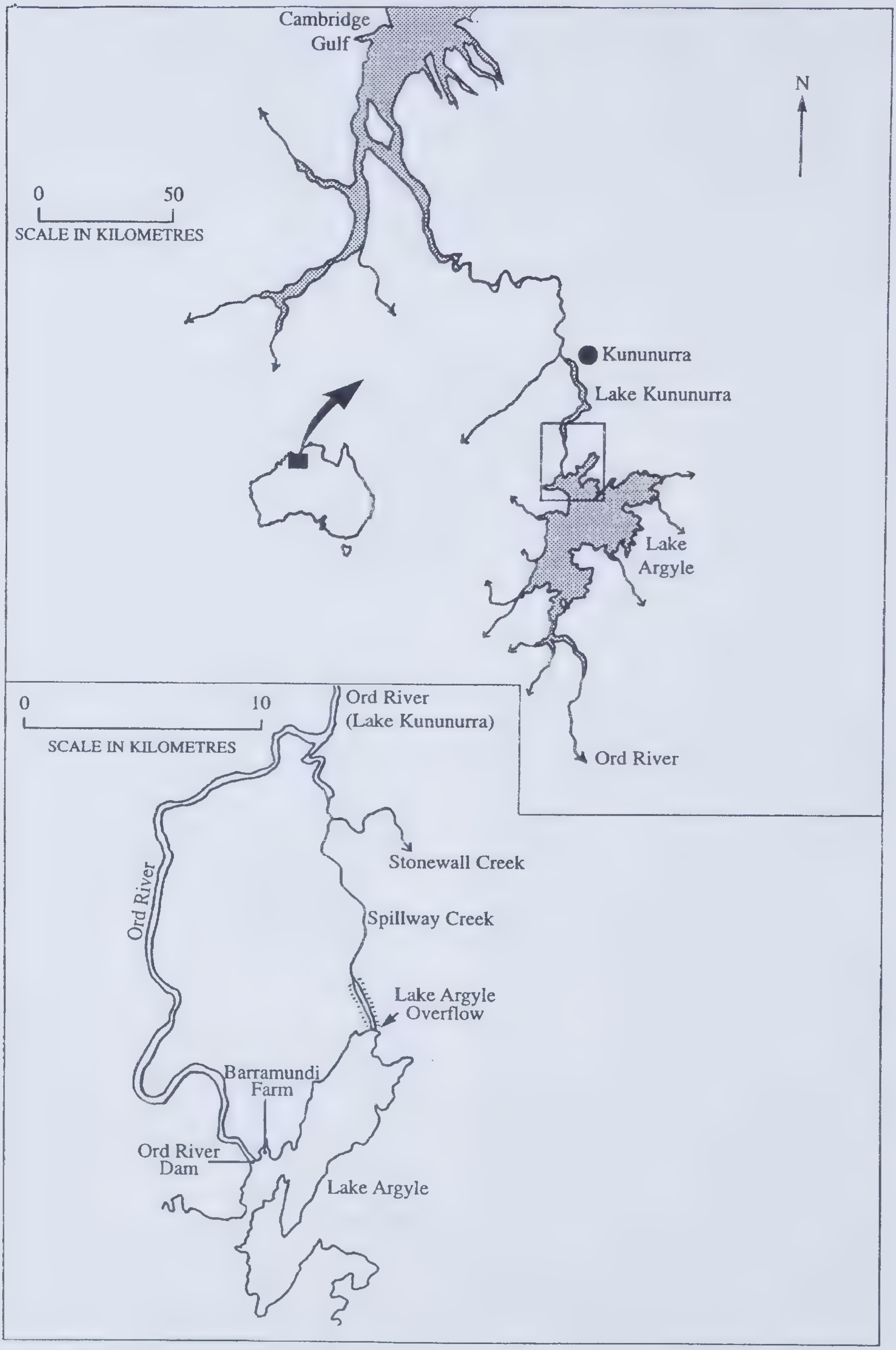

Figure 1. Geographic position of the Ord river system showing impoundments and locations of major study features.

barramundi in these impoundments. Either these fish were captured from the natural barramundi population below the diversion dam wall and have been released into Lake Kununurra, where they have moved upstream as part of their ecological migration, or they are cultured fish that have escaped from farm netpens into Lake Argyle and then into Spillway Creek. From these perspectives, this study aimed to compare the genetic identity of barramundi found in the impounded sections of the Ord River to cultured barramundi from the Lake Argyle fish farm.

Materials and Methods

Barramundi were sampled from the Lake Argyle barramundi farm (7 fish), from the open waters of Lake Argyle (8 fish) and from Spillway Creek (4 fish). For each fish, tissue samples comprising a caudal fin clip and/or muscle tissue (Doupé & Chandler 1998) were placed in specimen vials containing 80% ethanol for 2 hours. Once the alcohol had diffused through the tissue, it was replaced with 70% ethanol for sample storage. Samples were then transported to Perth and processed at the laboratories of the Centre for Human Genetics at Edith Cowan University, using the methods of Doupé & Chandler (1998) and Doupé *et al.* (1999).

Briefly, DNA was extracted from the tissue samples and primers described by Chenoweth *et al.* (1998) were used to amplify a 290 bp fragment within Region 1 of the barramundi mitochondrial control region by the polymerase chain reaction. The amplified product was sequenced using thermal cycle sequencing, interpreted with the aid of the Sequence Navigator 1.0.1 software package. Sequences from different fish were aligned by eye using MacClade 3.03 (Maddison & Maddison 1992).

Barramundi mtDNA control region sequences were compared among those localities surveyed in this study and with the wild population of the lower Ord River sampled by Doupé *et al.* (1999).

Results

This study identified a total of 19 barramundi mtDNA control region sequences, with each being 231 nucleotide bases in length. Two distinct mtDNA haplotypes were found (haplotypes A & B) and are shown in Table 1. Both haplotypes were detected at each locality; 5 A and 2 B haplotypes at the fish farm, 2 A and 6 B haplotypes in Lake Argyle, and 3 A and 1 B haplotypes in Spillway Creek. Neither the A nor the B haplotype found in this study was detected in the natural Ord River population sampled by Doupé *et al.* (1999).

Discussion

The Western Australian Department of Environmental Protection and Fisheries Western Australia are signatories to a Memorandum of Understanding concerning the translocation of aquatic species into Western Australia and between watersheds within Western Australia. Barramundi display significant population genetic structure eastwards from the Ord River in Western Australia (Shaklee *et al.* 1993; Keenan 1994; Chenoweth *et al.* 1998), and Doupé *et al.* (1999) showed substantial genetic differentiation between barramundi from the Kimberley (Ord and Fitzroy Rivers), Darwin and Cairns (Queensland). Since the depiction of Kimberley barramundi as a genetically differentiated stock, the proprietors at Lake Argyle have been encouraged to collect broodstock from the Ord River region, but the program is at a pilot stage and the Darwin hatchery remains the source of broodstock for the Lake Argyle fish farm.

Are barramundi escaping?

The identical mtDNA haplotypes found among barramundi of the fish farm, Lake Argyle and Spillway Creek provide strong evidence that barramundi have escaped from the farm at Lake Argyle. An alternative explanation is that they have migrated to Spillway Creek and Lake Argyle from the Ord River. Haplotypes A and B found in this study were not detected in the Ord River population sampled by Doupé *et al.* (1999). It is possible that haplotypes A and B are present in the natural Ord River population, but were missed by the sample of Doupé *et al.* (1999). Nevertheless, it seems a reasonable assumption that the haplotypes would occur no more frequently than $^1/_{14}$ or 0.07. If this is so, then the probability that the 8 fish sampled from Lake Argyle originated from the Ord River is $\leq 5.76\ 10^{-10}$ (0.07^8), and the probability that the 4 fish sampled from Spillway Creek originated from the Ord River is $\leq 2.40\ 10^{-5}$ (0.07^4) Clearly, these are highly unlikely events. The most parsimonious explanation, then, is that the fish in Lake Argyle and Spillway Creek escaped from the fish farm.

Hybridization between escaped and wild barramundi

The presence of escaped farmed fish in Spillway Creek suggests that they can potentially migrate from Lake Argyle to Lake Kununurra. A trial stocking of 124 tagged barramundi in Lake Kununurra recaptured fish from below the diversion dam (n = 9), and as far downstream as the Ord River estuary (C Bird, Fisheries Western Australia, pers comm). This indicates that barramundi can move from Lake Kununurra into the lower Ord River, and suggests that escaped cultured fish have the potential to genetically contribute to the natural Ord River population. The risk of hybridization then depends upon the rate of escape of cultured fish, how many survive to reproductive maturity, and then how many achieve reproductive success. The long-term effects of hybridization depend upon the effective population size (N_e) of the existing Ord River population, compared to the size of the cultured population that survives and contributes genetic material to it. N_e is extremely difficult to measure, but is usually very much smaller than the actual population size (Waples 1990). About 300-500 barramundi have been caught in Lake Argyle as a bycatch of the professional catfishery (C Ostle, Fisheries Western Australia, pers comm), and about 12-15 individual fish have been seen in Spillway Creek (Doupé, unpublished observations). How many have escaped beyond there into Lake Kununurra is not known.

The effect of hybridization on local adaptation

There is concern about genetic interaction between wild stocks and fish bred for aquaculture (Ryman 1991),

Table 1

Barramundi mtDNA control region sequences showing haplotypes A and B. A matching nucleotide base is indicated by "-". AL - Lake Argyle; SC - Spillway Creek; FF - Fish Farm.

A	AL2	TCAACATTTGCTTGTAATCAAAGGACATACGTGCATTCAATGGTACTCGTAAATGCAATGTACGGTAACCTATAATTAATGTACTTCAAGCAATAATATTACATACTGATCATCAGCAATAATATGAGCGTAGTGAGAGATCACCAATCAGTAGGTATTCAGAGTGTTGACGGTTCTTGATAGTCAAGGACAGATACGGTGTGGGGGTTACACAAATTGAACTATTACTGG
	AL6	---
	SC1	---
	SC3	---
	SC4	---
	FF1	---
	FF3	---
	FF4	---
	FF6	---
	FF7	---
B	AL1	C T C AT AC C CT A A C A A AA
	AL3	C T C AT AC C CT A A C A A AA
	AL4	C T C AT AC C CT A A C A A AA
	AL5	C T C AT AC C CT A A C A A AA
	AL7	C T C AT AC C CT A A C A A AA
	AL8	C T C AT AC C CT A A C A A AA
	SC2	C T C AT AC C CT A A C A A AA
	FF2	C T C AT AC C CT A A C A A AA
	FF5	C T C AT AC C CT A A C A A AA

including barramundi (Keenan & Salini 1990; Shaklee *et al.* 1993; Doupé 1997). There is a perceived risk that translocation of hatchery-reared fish could result in the establishment of less fit haplotypes, thus reducing stock fitness through the disruption of coadapted genomes (Keenan 1994). There is no clear relationship between the extent of genetic differences among populations and the degree of local adaptation; the issue is largely one of whether genetic differentiation has occurred through genetic drift or through selection (Johnson 2000).

Keenan (1994) thought that population genetic differentiation in barramundi is due to genetic drift as a result of small effective population sizes. There is, however, wide variability in life history traits among barramundi populations. For example, wild barramundi display geographic variation among localities for sex change (Moore 1979; Davis 1982), the presence of primary females (Moore 1979; Maneewong 1987), variable length/sex ratio relationships (Patnaik & Jena 1976; Moore 1979; Davis 1982) and the possibility of fully marine life histories (Pender & Griffin 1996). Such flexible life histories may be due to non-adaptive genetic differences or phenotypic plasticity, or they may be real adaptive differences. Much of the ecological diversity found among geographically disparate barramundi populations coincides with the population genetic differentiation found in the summary studies of Shaklee *et al.* (1993) and Keenan (1994). As yet, there is little ecological data for Kimberley barramundi (Doupé *et al.* 1999).

Stock management

Although demographic and ecological information is required if the influence of local selection pressures and population genetic differentiation are to be clarified, it has been argued that sustainable barramundi aquaculture in the Kimberley region of Western Australia should look toward the propogation of local stocks (Doupé 1997). However, the use of local stocks for culture will not necessarily safeguard the genetic integrity of the wild population. Aquaculturalists restrict the captive gene pool, either unintentionally through limited broodstock usage or by selecting for favoured production traits, like growth rate and disease resistance. The result of this artificial selection will be a captive population that is genetically divergent to its wild counterparts, irrespective of its origin.

The simplest and most pragmatic management approach would be to ensure that cultured fish do not escape. This could be achieved by requiring farms to provide better security, apart from predator nets, and by installing a mesh or netting mechanism at the Spillway Creek outlet that inhibited barramundi movement. A barramundi barrier at Spillway Creek would ideally be sized so as not restrict the movement of other aquatic species, such as black bream (*Hephaestus jenkinsi*), which are a significant component of the recreational fishery in Lake Kununurra, and the catfishes that support a small commercial fishery in its upper reaches. Further consideration should also be given to the expansion of commercial catfishing licences in Lake Argyle to allow the sale of barramundi caught as a bycatch; presently catfishermen are required to return all non-target species to the water.

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A comparison of gravimetric geoid models over Western Australia, computed using modified forms of Stokes's integral

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Abstract

Gravimetric models of the geoid over Western Australia have been constructed using two adapted forms of Stokes's integral; one uses the unmodified Stokes kernel and the other uses a deterministically modified kernel. These solutions use a combination of the complete expansion of the EGM96 global geopotential model with Australian gravity and terrain data. The resulting combined solutions for the geoid are compared with the control given by Global Positioning System (GPS) and Australian Height Datum heights at 63 points over Western Australia. The improved fit of the model that uses a modification to Stokes's kernel indicates that this approach is more appropriate for gravimetric geoid computations over Western Australia.

Introduction

The geoid is the equipotential surface of the Earth's gravity field, which corresponds most closely with mean sea-level (ignoring oceanographic effects) and undulates with respect to an oblate ellipsoidal model of the figure of the Earth. In 1849, GG Stokes published a solution to the geodetic boundary-value problem, which requires a global integration of surface gravity data over the Earth to compute the separation (*N*) between the geoid and reference ellipsoid (Stokes 1849). However, the incomplete global coverage and availability of accurate gravity measurements has precluded an exact determination of the geoid using Stokes's formula. Instead, an approximate solution is used in practice, where only gravity data in and around the computation area are used. This approach is also attractive because of the increase in computational efficiency that is offered by working with a smaller integration area.

In 1958, MS Molodensky (cited in Molodensky *et al.* 1962) proposed a modification to Stokes's formula to reduce the truncation error that results when gravity data are used over a limited area. However, Molodensky's modification did not receive a great deal of attention at that time because of the contemporaneous availability of low-frequency global gravity field information, derived from the analysis of the orbits of artificial Earth satellites. These global geopotential models are expressed in terms of fully normalised spherical harmonic functions and are now routinely used in conjunction with terrestrial gravity data via a truncated form of Stokes's integral (*e.g.* Vincent & Marsh 1973; Sideris & She 1995). This combined approach reduces the truncation error because its series expansion begins at a higher degree, where the truncation coefficients are smaller in magnitude (assuming that the global geopotential model is an exact fit to the low-degree terrestrial gravity field). Another advantage of this combined solution for the geoid is that it reduces the impact of the spherical approximation inherent to the derivation of Stokes's integral (*e.g.* Heiskanen & Moritz 1967), the reason being that most of the geoid's power is contained in the low frequencies.

This paper will briefly review the approaches currently used in regional gravimetric geoid computations and presents a compromise approach based on a high-degree global geopotential model and a low-degree modified Stokes kernel (Featherstone *et al.* 1998). An empirical comparison between gravimetric geoid models computed for Western Australia using the unmodified Stokes kernel and the compromise approach will be made with 63 discrete geoid heights. From these comparisons, it will be concluded that the compromise approach is more appropriate for gravimetric geoid computations in Western Australia.

The generalised Stokes scheme

A formal representation of the combination of a global geopotential model with terrestrial gravity data has been proposed by Vaníček & Sjöberg (1991), which they refer to as the generalised Stokes scheme for geoid computation. Importantly, this satisfies a solution to the geodetic boundary-value problem when formulated for a higher than second-degree reference model of the figure of the Earth (Martinec & Vaníček, 1996). In this scheme, the low-frequency geoid undulations generated by a global geopotential model (N_M) are extended into the high frequencies by a global integration of complementary high-frequency, terrestrial gravity anomalies (Δg^M) using

$$N = N_M + \kappa \int_0^{2\pi} \int_0^{\pi} S^M(\cos\psi)\, \Delta g^M \, \sin\psi \, d\psi \, d\alpha \qquad (1)$$

where $\kappa = R/4\pi\gamma$, R is the spherical Earth radius, γ is normal gravity evaluated on the surface of the geocentric reference ellipsoid as required by Bruns's formula (*e.g.* Heiskanen & Moritz 1967), ψ and α are the coordinates of spherical distance and azimuth angle about the computation point, respectively, and $S^M(\cos\psi)$ is the spheroidal form of Stokes's integration kernel, which is implicit to the generalised scheme and has the series expansion

$$S^M(\cos\psi) = \sum_{n=M+1}^{\infty} \frac{2n+1}{n-1} P_n(\cos\psi) \tag{2}$$

where $P_n(\cos\psi)$ is the n^{th} degree Legendre polynomial.

In Eq (1), the low-frequency component of the geoid (N_M) is computed from the fully normalised spherical harmonic coefficients that define the global geopotential model according to

$$N_M = \frac{GM_e}{r\gamma} \sum_{n=2}^{M} \left(\frac{a}{r}\right)^n \sum_{m=0}^{n} (\delta\overline{C}_{nm}\cos m\lambda + \overline{S}_{nm}\sin m\lambda)\overline{P}_n^m(\cos\theta) \tag{3}$$

The corresponding high-frequency gravity anomalies (Δg^M) are evaluated by subtracting the same spherical harmonic degrees of the same global geopotential model from the terrestrial gravity anomalies (Δg) according to

$$\Delta g^M = \Delta g - \frac{GM_e}{r^2} \sum_{n=2}^{M} \left(\frac{a}{r}\right)^n (n-1) \sum_{m=0}^{n} (\delta\overline{C}_{nm}\cos m\lambda + \overline{S}_{nm}\sin m\lambda)\overline{P}_n^m(\cos\theta) \tag{4}$$

In Eqs (3) and (4), GM_e is the product of the Newtonian gravitational constant and mass of the solid Earth, oceans and atmosphere, a is the equatorial radius of the reference ellipsoid, (r, θ, λ) are the geocentric spherical polar coordinates of each computation point, $\delta\overline{C}_{nm}$ and $\overline{S}_{nm}$ are the fully normalised geopotential coefficients of degree n and order m, which have been reduced by the even zonal harmonics of the reference ellipsoid, and $\overline{P}_{nm}(\cos\theta)$ are the fully normalised associated Legendre functions. It is assumed that the reference ellipsoid is geocentric and has the same mass, potential and rotation rate as the geoid, such that the zero and first degree harmonics are inadmissible (*e.g.* Heiskanen & Moritz 1967).

The degree (M) of reference spheroid chosen for the generalised Stokes scheme can be driven by the maximum degree of global geopotential model available, which is usually $M_{max} = 360$. However, there are more important considerations than simply taking the maximum degree of expansion available (*e.g.* Featherstone 1992). Firstly, the $M_{max} = 360$ models are already combined solutions for the geoid because they are constructed from both satellite-derived and terrestrial gravity data. Therefore, the same terrestrial gravity data are usually used twice in Eq (1), which gives rise to unknown correlations between these data that are rarely accounted for or even acknowledged by some authors. Another consideration is the leakage of low-frequency errors from the terrestrial gravity anomalies into the combined solution for the geoid, which can be filtered by the spheroidal kernel due to the orthogonality of spherical harmonic functions over the sphere (*e.g.* Vaníček & Featherstone 1998). This is considered to be a desirable scenario because the low-frequency geopotential coefficients are currently the best source of this information, whereas terrestrial gravity data are subject to low-frequency errors. Therefore, choosing the degree of spheroid at, say, $M = 20$ in Eq (1), which is the limit of the reliable resolution of the satellite-derived geopotential coefficients, both avoids the correlations and reduces the leakage of terrestrial gravity anomaly errors.

Reduction of the Approximation Error

The generalised Stokes scheme

The generalised Stokes scheme (Eq 1) remains subject to a truncation error when high-frequency terrestrial gravity anomalies are used over a limited area. Accordingly, there is an adjustment of Eq (1) that involves limiting the integration domain to a spherical cap of radius ψ_0 ($0 \le \psi_0 \le \pi$) about each geoid computation point, which yields the approximation

$$N \simeq \hat{N}_1 = N_M + \kappa \int_0^{2\pi} \int_0^{\psi_o} S^M(\cos\psi)\, \Delta g^M \, \sin\psi \, d\psi \, d\alpha \tag{5}$$

with a corresponding truncation error of

$$\delta N_1 = \kappa \int_0^{2\pi} \int_{\psi_o}^{\pi} S^M(\cos\psi)\, \Delta g^M \, \sin\psi \, d\psi \, d\alpha \tag{6}$$

such that $N = \hat{N}_1 + \delta N_1$. This truncation error can be expressed as a series expansion by

$$\delta N_1 = 2\pi\kappa \sum_{n=M+1}^{\infty} Q_n^M(\psi_o)\, \Delta g_n \tag{7}$$

where the spheroidal truncation coefficients

$$Q_n^M(\psi_o) = \int_{\psi_o}^{\pi} S^M(\cos\psi)\, P_n(\cos\psi)\, \sin\psi \, d\psi \tag{8}$$

can be evaluated using the algorithms of Paul (1973). The n^{th} degree surface spherical harmonic of the gravity anomaly can be evaluated for each n up to the maximum degree (M_{max}) of the geopotential model using

$$\Delta g_n = \frac{GM}{r^2} \left(\frac{a}{r}\right)^n (n-1) \sum_{m=0}^{n} (\delta\overline{C}_{nm}\cos m\lambda + \overline{S}_{nm}\sin m\lambda)\overline{P}_n^m(\cos\theta) \tag{9}$$

As such, the truncation error in Eq (7) reduces to

$$\delta N_1 = 2\pi\kappa \sum_{n=M_{max}+1}^{\infty} Q_n^M(\psi_o)\, \Delta g_n \tag{10}$$

However, if $\Delta g^M \neq 0$ ($2 \le n \le M$), which is true if the global geopotential model is not an exact fit to the low-frequency terrestrial gravity anomalies, Eq (10) no longer holds and there is a leakage of any low-frequency gravity errors into the geoid solution when the integration is performed over a limited area (Vaníček & Featherstone 1998). This is a direct consequence of the approximation of the generalised Stokes integral, which introduces the non-zero truncation coefficients in the region $2 \le n \le M$ because the orthogonality of spherical harmonics over the sphere breaks down under the approximation in Eq (5). Since Δg_n only depend on the physical properties of the Earth, it becomes necessary to seek a modification to the integration kernel that reduces the magnitude of the truncation coefficients and hence the truncation error. Ideally, this modification should reduce the truncation error as well as adapting the kernel to behave as a (partial) high-pass filter and thus reduce the leakage of any low-frequency terrestrial gravity data errors into the geoid (Vaníček & Featherstone 1998).

The remove-compute-restore scheme

The remove-compute-restore technique (*e.g.* Torge 1991) has almost become a standard approach in regional combined solutions for the geoid. However, most users of this approach make no attempt to modify the integration kernel and thus (further) reduce the truncation error or adapt its filtering properties. Instead, this scheme uses the unmodified kernel as originally introduced by Stokes (*e.g.* Sideris & She 1995; Smith & Milbert 1999). The remove-compute-restore approach also generally uses the maximum available degree of the global geopotential model (M_{max}), which gives rise to the approximated data combination

$$N \simeq \hat{N}_2 = N_{M_{max}} + \kappa \int_0^{2\pi} \int_0^{\psi_0} S(\cos\psi)\, \Delta g^{M_{max}} \sin\psi \, d\psi \, d\alpha \tag{11}$$

where the terms N_{Mmax} and Δg^{Mmax} are computed from the maximum available degree and order of a global geopotential model (Eqs. 3 and 4), and the unmodified Stokes kernel is given by

$$S(\cos\psi) = \sum_{n=2}^{\infty} \frac{2n+1}{n-1} P_n(\cos\psi) \tag{12}$$

In this combined solution for the geoid, the truncation error for degrees greater than M_{max} has to be neglected because it cannot be computed since the complete expansion of the global geopotential model has already been used. This also makes it subject to the correlation of errors between the global geopotential model and terrestrial gravity data used in the regional geoid solution. Moreover, no other attempt has been made to reduce the truncation error or adapt the filtering properties of the integration kernel. Admittedly, the truncation error will reduced a great deal if the global geopotential model is a good fit to the terrestrial gravity anomalies in the area of interest (*i.e.* if $\Delta g^M = 0$ in the region $2 \leq n \leq M_{max}$). However, the penalty of taking this approach is that any errors in the terrestrial gravity anomalies to propagate unattenuated into the combined solution for the geoid (Vaníček & Featherstone 1998). It must also be acknowledged that, despite these restrictions, the remove-compute-restore technique has delivered quite reasonable results (*e.g.* Sideris & She 1995; Smith & Milbert 1999). However, the question of whether a modified integration kernel in the generalised Stokes scheme will deliver even better results remains, and thus forms the primary aim of this investigation.

Integration kernel modifications

As argued above, it remains preferable to apply a modification to the approximated form of the generalised Stokes's integral (Eq 5) and the remove-compute-restore approach (Eq 11) so as to further reduce the associated truncation error. Since Molodensky's pioneering work, several other authors have proposed modifications to Stokes's (1849) integral. These have been based on different criteria and can be broadly classified as deterministic modifications (*e.g.* Molodensky *et al.* 1962; Wong & Gore 1969; Meissl 1971; Heck & Grüninger 1987; Vaníček & Kleusberg 1987; Vaníček & Sjöberg 1991; Featherstone *et al.* 1998) and stochastic modifications (*e.g.* Wenzel 1982; Sjöberg 1991; Vaníček & Sjöberg 1991). The stochastic modifications, whilst offering an optimal combination of the two data types together with a minimisation of the truncation error (in a least-squares sense), require reliable variance estimates of the data. However, the error characteristics of the terrestrial gravity data over Western Australia and over most other parts of the world are currently unknown, which renders the stochastic modifications of limited practical use. Therefore, the deterministic kernel modifications will have to be relied upon in the interim.

The deterministic kernel modifications can be further divided into two broad categories; modifications that reduce the upper bound of the truncation error according to some prescribed norm, and modifications that improve the rate of convergence of the series expansion of the truncation error. The modification proposed by Featherstone *et al.* (1998) uses a combination of these, where the rate of convergence of the series expansion of an already-reduced truncation error by the L_2 norm (Vaníček & Kleusberg 1987) is accelerated from $O(n^{-1})$ to $O(n^{-2})$ through the approach proposed by Meissl (1971). This can be achieved either by setting the kernel to zero at the truncation radius through subtraction, or by choosing the truncation radius such that it coincides with a zero point of the kernel.

The Featherstone *et al.* (1998) modification is given by

$$S_L^M(\cos\psi) = S^M(\cos\psi) - S^M(\cos\psi_0) - \sum_{k=2}^{L} \frac{2k+1}{2} t_k(\psi_0)\left[P_k(\cos\psi) - P_k(\cos\psi_0)\right] \tag{13}$$

where the $t_k(\psi_0)$ modification coefficients are computed from the solution of the following set of L-1 linear equations, once the truncation radius (ψ_0) has been chosen

$$\sum_{k=2}^{L} \frac{2k+1}{2} t_k(\psi_0)\, e_{nk}(\psi_0) = Q_n^M(\psi_0) \tag{14}$$

where the coefficients $Q^M{}_n(\psi_0)$ are given by Eq (8), and

$$e_{nk}(\psi_0) = \int_{\psi_0}^{\pi} P_n(\cos\psi)\, P_k(\cos\psi) \sin\psi \, d\psi \tag{15}$$

which can be evaluated using the recursive algorithms of Paul (1973). The degree of this kernel modification (L) can be chosen to be greater than, equal to or less than the degree of the reference spheroid (M) embedded in the generalised Stokes formula (Eq 1). If $L > M$, additional terms arise due to this disparate combination and should be computed or their omission acknowledged.

A compromise of the combined solution

The combined solution for the geoid considered in this study attempts to reach a compromise of the above two schemes, based on considerations of the data availability, their expected reliability, and a reduction of the truncation error through the above deterministic modification of the generalised Stokes kernel. This compromise approach was used to compute the recent Australian gravimetric geoid model, AUSGeoid98 (Johnston & Featherstone 1998). Mathematically, this is formalised as

$$N \simeq \hat{N}_3 = N_{M_{max}} + \kappa \int_0^{2\pi} \int_0^{\psi_0} S_L^M(\cos\psi)\, \Delta g^{M_{max}} \sin\psi \, d\psi \, d\alpha \tag{16}$$

where all terms are as defined earlier. Equation (16) utilises the maximum available expansion (M_{max}) of the global geopotential model in conjunction with a low-degree (L) of deterministic kernel modification. This approach aims at reducing the truncation error so that it can be safely ignored, whilst relying more on the low-degree satellite solution by filtering a proportion of the low-frequency errors from the terrestrial gravity data (*cf.* Vaníček & Featherstone 1998). However, this choice is also driven by some practical considerations. Empirical studies by Featherstone (1992) indicate that the modified kernels become numerically unstable for large L and small ψ_0, which enforces a low degree of kernel modification when a small integration radius is used. For simplicity, the degree of kernel modification is chosen equal to the degree of spheroid used in the generalised scheme (*i.e.* $L = M = 20$). The integration radius was chosen to be $\psi_0=1°$, since this value was empirically selected for AUSGeoid98 (Johnston & Featherstone 1998).

It is argued that this compromise approach offers a geoid solution that is superior to the application of the remove-compute-restore technique with an unmodified kernel because of its further reduction of the truncation error and adaption of the filtering properties of the kernel. However, it is also important to acknowledge the deficiencies of this attempted compromise, which are the use of the high-frequencies in the global geopotential model (which can contain 80% noise; *e.g.* Lemoine *et al.* 1998) and the correlations between the terrestrial gravity data in the region $20 < n \leq M_{max}$. Therefore, empirical tests are used in Western Australia to determine whether the use of a deterministically modified integration kernel is more appropriate than using the unmodified kernel.

Empirical tests in Western Australia

The tests that follow compare four combined solutions for the geoid, computed using differing parameters in Eqs (11) and (16), with discrete geoid heights at 63 points across Western Australia. These control data are derived from Global Positioning System (GPS) measurements at Australian Height Datum (AHD) benchmarks. The difference between a GPS-derived ellipsoidal height and geodetically levelled height with respect to mean sea level gives a discrete estimate of the separation between the geoid and reference ellipsoid. Assuming that there are no errors in these control data, the gravimetric geoid solution that delivers the best fit can be considered to be the most suitable for Western Australia.

Data and its processing

The EGM96 global geopotential model (Lemoine *et al.* 1998), complete to $M_{max} = 360$, was used in this study. EGM96 is one of the most recent global geopotential models and was produced by the US National Imagery and Mapping Authority (NIMA), formerly the Defense Mapping Agency (DMA), and the US National Aeronautical and Space Administration's (NASA) Goddard Space Flight Center (GSFC). Kirby *et al.* (1998) compared EGM96 with Australian gravity data (described below) and discrete geoid heights provided by co-located GPS and AHD data (also described below). This showed that EGM96 provides a slightly better (though statistically not significant) representation of the Australian gravity field than its predecessors.

The Australian Geological Survey Organisation's (AGSO) 1996 national gravity data release, being the most recent available to the author, has been used in the computations. As most of the AGSO gravity data were collected and reduced predominantly for geophysical exploration purposes, they are not necessarily suited to the requirements of gravimetric geoid computation. As such, they have been validated according to the procedures in Featherstone *et al.* (1997) and the gravity anomalies computed using the more stringent geodetic approaches (*e.g.* Featherstone & Dentith 1997). Deficiencies were also found in the mean free-air gravity anomalies computed on land, due to the gravity data collection strategies used by AGSO. The land gravity observations were typically made along roads and tracks in areas of rugged terrain, which usually follow valleys or areas of least height variation. A similar, though opposite, effect occurs in central Australia where most observations were performed using helicopter transport. These observations were often located on raised ground where convenient landing spots were identified. Specifically, the computed mean gravity anomaly does not truly represent the actual mean gravity anomaly of an area. As such, the computed gravimetric geoid is biased by these gravity observation techniques. To numerically counter this biasing effect, a digital elevation model (described below), which gives a better representation of the mean terrain height than the gravity observation elevations, was used to reconstruct more representative mean gravity anomalies (Featherstone & Kirby 2000).

Satellite-altimeter-derived marine gravity anomalies were used offshore Australia to supplement AGSO's marine gravity data coverage. These gravity anomalies were computed from a combination of satellite-borne radar altimeter missions and supplied on a 2' by 2' geographical grid (Sandwell & Smith 1997). These data significantly improve the gravity data coverage offshore Australia and, as such, were expected to give an improved geoid solution in marine areas and on land areas close to the coast. However, errors thought to reside in the low-frequency altimeter-derived gravity anomalies adversely affect the gravimetric geoid near the coast, which was indicated by comparisons of the geoid solution with GPS and AHD data on land near the coast. The low-frequency errors in the satellite altimeter data are probably due to a combination of poorly-modelled near-shore sea-surface topography, tides and backscatter of altimeter returns from the land. Another explanation for this observed deficiency comes from the conversion of sea surface heights, which are the direct measurements taken by the altimeter, to gravity anomalies, then converting these gravity anomalies to geoid heights. At present, it is unknown how the errors, such as poorly-modelled sea-surface topography, propagate through these processes. Therefore, as an interim and practical solution, least squares collocation (*e.g.* Moritz 1980a) was used to 'drape' the altimeter gravity anomalies onto the AGSO marine gravity anomalies (Kirby & Forsberg 1998). This approach then improved the geoid solution on land near the coast, when compared with GPS and AHD data, over that achieved using only the AGSO marine gravity data or simple averaging of the AGSO marine gravity data and the satellite-altimeter data.

Gravimetric terrain corrections, based on the national 9" by 9" digital elevation model (Carrol & Morse 1996), were evaluated using Moritz's (1968) formula via the fast Fourier transform or FFT (Kirby & Featherstone 1999). The FFT offers the only practical way to compute detailed terrain corrections on a continental scale, since prism integration at this scale could take several months to evaluate. It was found by Kirby & Featherstone (1999) that the terrain correction computations had to be performed using a 27" by 27" grid to avoid the instability in Moritz's terrain correction algorithm that occurs when using high-resolution digital terrain models close to the computation point (*cf.* Martinec *et al.* 1996). Associated with the gravimetric terrain correction are the primary and secondary indirect effects (*e.g.* Wichiencharoen 1982). The primary indirect effect accounts for the change in potential caused by the free-air gravity reduction and gravimetric terrain correction. The primary indirect effect was computed using the FFT on a 27" grid, which avoids the kernel instability and, moreover, is consistent with the terrain correction computations. The secondary indirect effect on gravity was computed by applying the free-air reduction over the geoid-compensated-geoid separation computed via the primary indirect effect. This resulted in an additional gravity term that was added to the gravity anomalies prior to geoid computation.

A grid of residual gravity anomalies was computed from the AGSO gravity observations using the continuous curvature spline in tension algorithm (Smith & Wessel 1990; Wessel & Smith 1995). The term residual gravity anomalies is used to describe the terrain-corrected free-air gravity anomalies that have been reduced by the gravity anomalies implied by the complete $M_{max} = 360$ expansion of EGM96 (Eq 4). A regular grid of residual gravity anomalies is required for the residual geoid computations via the one-dimensional FFT technique. It is acknowledged that other gravity gridding techniques exist, such as least squares collocation (Moritz 1980a), but the continuous curvature spline in tension algorithm was readily available (Wessel & Smith 1995) and gives almost identical results in a considerably shorter computation time (Zhang 1997). For this study, a 2' by 2' grid of gravity anomalies was generated over the region by $-11° \le \phi \le -37°$ and $110° \le \lambda \le 131°$, which covers the state of Western Australia. Table 1 summarises the statistical properties of the gravity anomalies and the residual gravity anomalies. The GRS80 reference ellipsoid (Moritz 1980b) has been used in all computations. Grey-scale images of the EGM96-implied gravity anomalies and residual gravity anomalies are shown in Figs 1 and 2, respectively.

The statistical fit of the gravity anomalies implied by the EGM96 global geopotential model to the gravity field of Western Australia is poorer than that experienced in other parts of the world (*cf.* Forsberg & Featherstone 1998). This is probably due to the larger uncertainty in the terrestrial gravity anomalies, which is caused principally by errors in the gravity station elevations (*e.g.* Featherstone *et al.* 1997). However, since a large proportion of these data has been used in the construction of the EGM96 global geopotential model, a more likely explanation is an inaccuracy in the mean gravity anomalies used

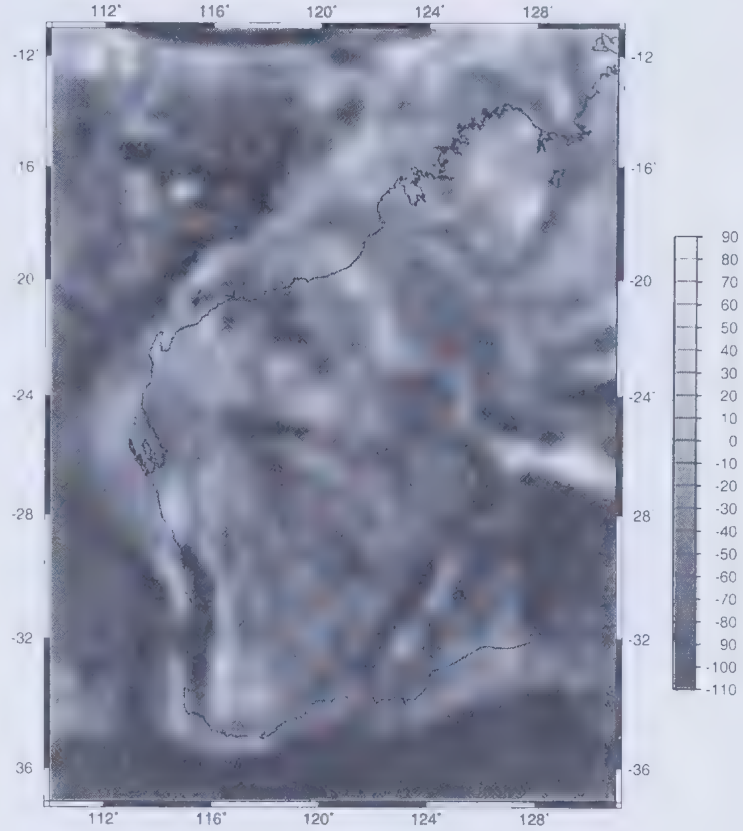

Figure 1. The M_{max} = 360 EGM96-implied gravity anomalies over Western Australia (units in mGal; Mercator's projection from the GRS80 ellipsoid).

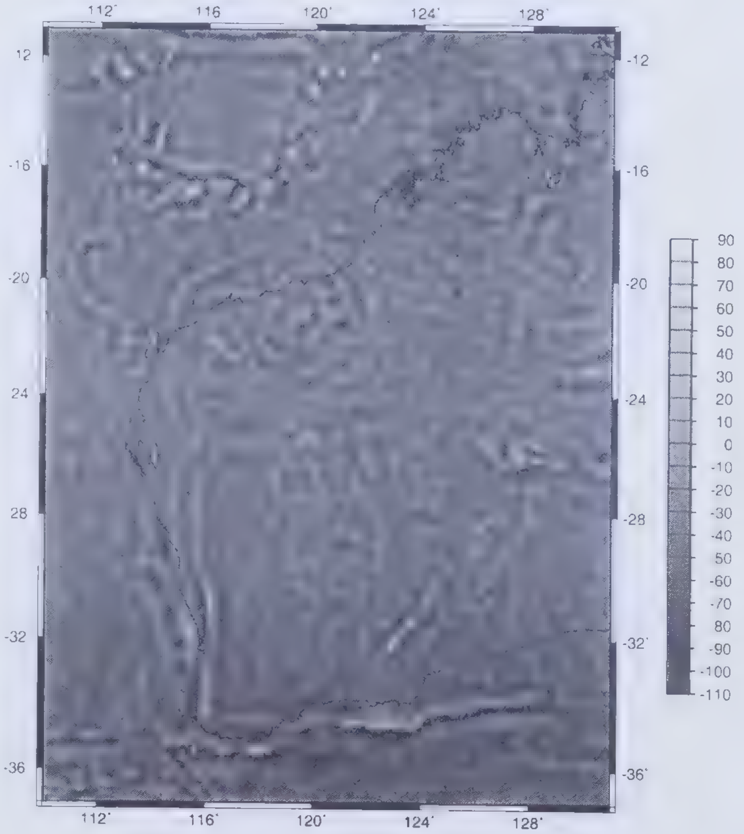

Figure 2. The residual gravity anomalies over Western Australia (units in mGal; Mercator's projection from the GRS80 ellipsoid).

Table 1

Minimum, maximum, mean, standard deviation (SD) and root mean square (RMS) for the gravity anomalies over Western Australia (units in mGal).

gravity anomalies	Minimum	Maximum	Mean	SD	RMS
terrain-corrected free-air	131.085	-147.678	-8.762	± 29.110	± 30.400
residual	91.554	-101.236	0.009	± 10.968	± 10.968

for this model. Lemoine *et al.* (1998) describe the construction of the JGP95E 5' by 5' digital elevation model, where the Australian 5' by 5' digital elevation model was used west of $\lambda = 140°$ and a National Imagery and Mapping Agency (NIMA) digital elevation model was used east of $\lambda = 140°$. The Australian 5' by 5' digital elevation model used by NIMA was probably that constructed at the Australian National University from the elevations associated with the gravity station elevations. Featherstone & Kirby (2000) show that this digital elevation model is biased because the gravity observations do not accurately represent the topographic morphology (see earlier discussion). Therefore, more reliance should be placed on the terrestrial gravity anomalies described earlier, hence the use of a low-degree kernel modification.

Geoid computation by the 1D-FFT technique

In the mid 1980s, the fast Fourier transform (FFT) technique began to find wide-spread use in gravimetric geoid computation, because of its efficient evaluation of convolution integrals when compared to quadrature-based numerical integration. For many years, the planar, two-dimensional FFT was used (*e.g.* Schwarz *et al.* 1990). Strang van Hees (1990) then introduced the spherical, two-dimensional FFT. However, both of these FFT approaches are subject to approximation errors, the most notable of which is the simplification of Stokes's kernel. Forsberg & Sideris (1993) therefore proposed the spherical, multi-band FFT, which reduces the impact of the simplified kernel. Haagmans *et al.* (1993) then refined this approach to give the spherical, one-dimensional FFT, which requires no simplification of Stokes's kernel. For this reason, the 1D-FFT has been used in this investigation so that the exact kernels in Eqs (12) and (13) can be used efficiently and without the need for any simplification.

Another consideration is that remove-compute-restore determinations of the geoid using the 1D-FFT often convolve the whole rectangular grid of gravity anomalies over a region with the spherical Stokes kernel (*e.g.* Sideris & She 1995; Smith & Milbert 1999). On the other hand, quadrature-based geoid determinations only use gravity anomalies over a spherical integration radius about each computation point. Therefore, each approach results in a different truncation error due to the neglect of the residual gravity anomalies in the (different shaped) remote zones outside each integration domain. Both of these implementations are tested in this study, where in Eq (11) the spherical integration radius is set to $\psi_0 = \pi$ so as to use the whole gravity data rectangle, and a limited spherical cap is used to mimic quadrature-based numerical integration.

In order to make the 1D-FFT approach closely mimic quadrature-based numerical integration over a spherical cap, the integration kernel is set to zero outside the truncation radius ($\psi_0 = 1°$) before transformation to the frequency domain. A further adaptation of this technique has been added to allow the 1D-FFT-based evaluation of Eq (16), where the modified kernel (Eq 13) was implemented by evaluating it before transformation to the frequency domain (Featherstone & Sideris 1998). Comparisons with quadrature-based numerical integration software that uses spherical caps and deterministically modified integration kernels (Featherstone, 1992) were used to verify these adaptations of the 1D-FFT.

In what follows, the gravimetric geoid heights from each approach have been evaluated using the 1D-FFT for

(i) the remove-compute-restore technique with an unmodified kernel and residual gravity anomalies over whole data area $\psi_0 = \pi$,

(ii) the remove-compute-restore technique with an unmodified Stokes's kernel and residual gravity anomalies over a limited spherical cap ($\psi_0 = 1°$), and

(iii) the compromise approach in Eq (16) with a deterministically modified kernel and residual gravity anomalies over a limited spherical cap ($\psi_0 = 1°$).

In the latter case, the degree of spheroid associated with the generalised Stokes scheme is $M = 20$ and the degree of deterministic kernel modification is the same. Of course, a large number of permutations of these parameters is possible by varying the degree of global geopotential model (M), integration radius (ψ_0), degree of kernel modification (L), and even the type of kernel modification (see section Integration Kernel Modifications, above). However, only the above three cases are studied for Western Australia because the remove-compute-restore technique is used in many other parts of the world (*e.g.* Sideris & She 1995; Smith and Milbert 1999), and the $L = M = 20$ modification for a cap radius of $\psi_0 = 1°$ was used for AUSGeoid98 (Johnston & Featherstone 1998).

All geoid computations were conducted on a 2' by 2' grid over an area bound by $-12° \leq \phi \leq -36°$ and $112° \leq \lambda \leq 129°$, which eliminates the edge effect associated with the one-degree integration radius (with the exception of the integration over the whole data area). It should be pointed out that this edge effect affects the whole computation area when the cap-radius is unlimited. Nevertheless, the geoid comparisons are conducted over the same area for the sake of consistency.

Comparison of Geoid Results with GPS at AHD Benchmarks

As is customary in almost all validations of gravimetric geoid models on land, the geoid results from this study were compared with Global Positioning

System (GPS) and geodetic levelling data to determine if any improvements are made when utilising a spherical integration cap and deterministically modified kernel. However, it must be pointed out this type of comparison is inevitably biased because the geodetic levelling data used in this investigation are based on the Australian Height Datum (AHD). The AHD is a normal orthometric height system based on estimates of mean sea level from 30 tide gauges around Australia (Roelse *et al.* 1971). As such, it does not give an exact representation of the equipotential geoid (*e.g.* Featherstone 1998). Nevertheless, GPS and geodetic levelling data currently provide the only (partially) independent means with which to verify a gravimetric geoid model on land. Given that the primary geodetic application of a gravimetric geoid model is to transform GPS-derived ellipsoidal heights to the AHD, this type of analysis is also useful to ascertain the gravimetric geoid models' performance for this application.

For each of the three cases investigated, the gravimetric geoid solution was bi-cubically interpolated from the 2' by 2' grid and statistically compared with 63 discrete geoid heights. These were derived geometrically from the most precise GPS networks available in Western Australia (Morgan *et al.* 1996; Stewart *et al.* 1997) at points that are co-located with geodetically levelled heights of third-order, or better, on the AHD. Table 2 shows a statistical summary of the differences between the 63 control geoid heights and the results from the M_{max}=360 expansion of EGM96 alone (Eq 3), the 1D-FFT implementations of Eq (11) with $\psi_0 = \pi$ and $\psi_0 = 1°$, and Eq (16) with $\psi_0 = 1°$. The mean and root mean square (RMS) differences in Table 2 should not be relied upon to choose the most accurate geoid solution because any gravimetric determination of the geoid is deficient in scale (*i.e.* only the gravimetric geoid's precision can be estimated). This scale deficiency due to the imperfect knowledge of the mass of the Earth [*cf* the text immediately after Eqs (3) and (4)]. Accordingly, only the standard deviations of the fit of each gravimetric geoid model to the control data should be used to assess the performance in terms of precision of each model; the mean and RMS values are only included for the sake of completeness.

The difference between the fit of each geoid model in Table 2 is not always significant in a statistical sense, when considering that the random error budget of the GPS data is ~0.05 m (Morgan *et al.* 1996; Stewart *et al.* 1997) and distortions of the AHD from the geoid are of the order of 1 m (Roelse *et al.* 1971; Featherstone & Stewart 1998; Featherstone 1998). Despite these caveats, some useful inferences can be made from these results as follows.

Firstly, the use of the whole gravity data area in the combined solution for the geoid (Eq 11 with $\psi_0 = \pi$) gives a result that is worse than using the EGM96 global geopotential model alone (Table 2). Whilst the use of the whole data area appears to be appropriate in other parts of the world (*e.g.* Sideris & She 1995; Smith & Milbert 1999), a considerably worse result is achieved in Australia when using this approach (Table 2; Forsberg & Featherstone 1998; Johnston & Featherstone 1998). This is a slightly unexpected result, since including more data in the geoid solution should yield a better result. This is either due to noise in the Australian gravity anomalies, which been estimated to be approximately ± 2 mGal (Featherstone *et al.* 1997), or the theoretical basis of this approach is unsuitable for Australia.

Next, from Table 2 there is an improvement over the results of using only the EGM96 global geopotential

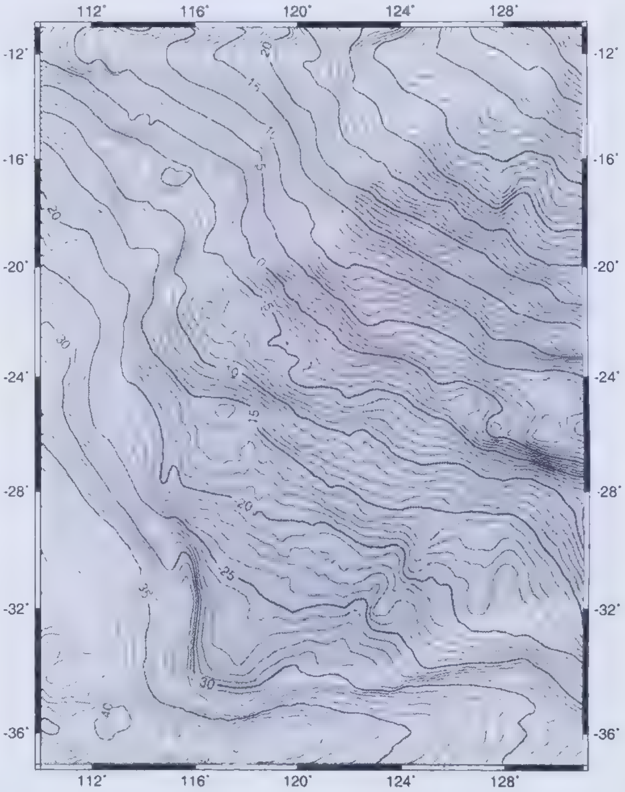

Figure 3. The gravimetric geoid over Western Australia, computed using Eq (16) with $\psi_0 = 1°$ and $S_{20}^{20}(\cos\psi)$; units in metres; Mercator's projection from the GRS80 ellipsoid.

Table 2

Minimum, maximum, mean, standard deviation (SD) and root mean square (RMS) for the absolute between the 63 control GPS-AHD heights and the gravimetric geoid heights computed from EGM96 only, Eq (11) with $\psi_0 = \pi$ and $\psi_0 = 1°$ and Eq (16) with $\psi_0 = 1°$ (units in metres).

	Minimum	Maximum	Mean	SD	RMS
M_{max} = 360 expansion of EGM96 (Eq 3)	0.889	-0.328	0.148	± 0.274	± 0.311
Eq (11) with ψ_0 = p and $S(\cos\psi)$	0.751	-0.776	-0.092	± 0.362	± 0.374
Eq (11) with $\psi_0 = 1°$ and $S(\cos\psi)$	0.625	-0.664	0.118	± 0.249	± 0.276
Eq (11) with $\psi_0 = 1°$ and $S_{20}^{20}(\cos\psi)$	0.761	-0.308	0.140	± 0.223	± 0.263

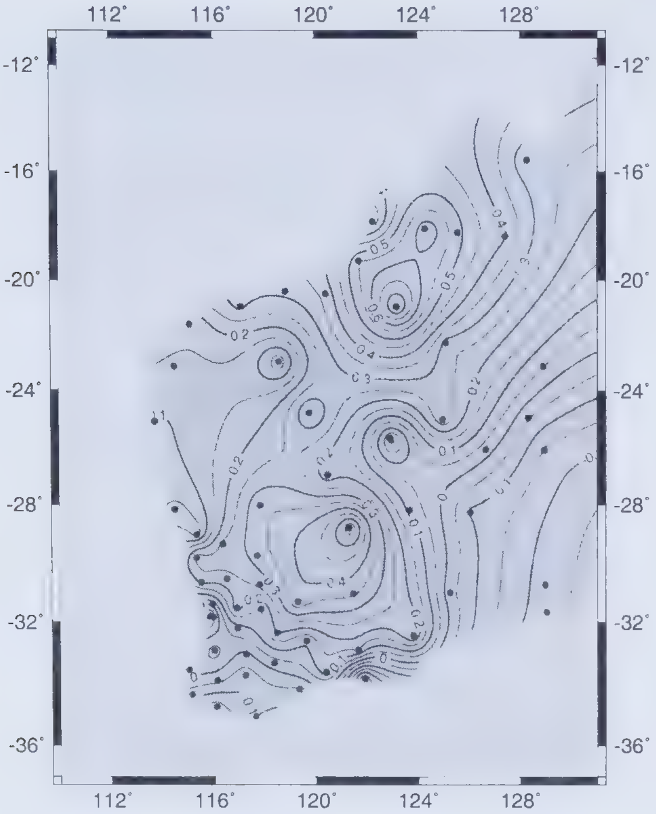

Figure 4. The differences between the 63 GPS-AHD discrete geoid heights (circles) and the gravimetric geoid (Fig 3); units in metres; Mercator's projection from the GRS80 ellipsoid.

model offered by the use of a limited integration radius in Eq (11). Importantly, there is a further improvement offered by using the deterministically modified integration kernel in Eq (16) for the same integration radius. Though inconclusive due to the perceived uncertainties in the control data, these results do indicate that the use of deterministically modified integration kernel is a preferable approach for geoid computations in Western Australia. This is bearing in mind that the principal application of the gravimetric geoid in Australia is to transform GPS-derived ellipsoidal heights to the AHD. Fig 3 shows a contour map of the gravimetric geoid model of Western Australia that has been computed using Eq (16) with $\psi_0 = 1°$ and $L = M = 20$.

Finally, it is informative to view the geographical distribution of the discrepancies between the 63 GPS-AHD discrete geoid heights and the gravimetric geoid computed from the modified Stokes integral (Fig 4). There are systematic differences between the gravimetric geoid and the control data, where these features (highs, lows and slopes) are defined by more than one control point. Given the relatively small error budget of the GPS data (≈ 0.05 m), it becomes difficult to ascertain whether these systematic differences are due to distortions in the AHD, the gravimetric geoid, or both. It is currently impossible to isolate the exact source, but following the arguments in Featherstone & Stewart (1998), it is more likely that these errors are due to distortions in the AHD. These are introduced because the AHD is constrained to mean sea level observed over two years at 30 tide gauges around Australia (Roelse *et al.* 1971) and thus does not necessarily represent an equipotential surface of the Earth's gravity field (Featherstone 1998). However, the possibility of systematic errors in the gravimetric geoid cannot be ruled out as an explanation for these discrepancies.

Conclusion

From these gravimetric geoid results over Western Australia, it is clear that 1D-FFT geoid computations should use a spherical cap of limited extent instead of the whole gravity data grid. Small (though not statistically significant when considering the errors in the GPS and AHD data) improvements are also observed when a deterministically modified integration kernel is used over a spherical cap in the compromise approach to gravimetric geoid determination (Eq 16). This improvement is probably because the kernel modification reduces the truncation error so that its neglect has less impact on the solution and adapts the filtering properties of the kernel thereby reducing the effect of low-frequency terrestrial gravity anomaly errors. Therefore, it is recommended that limited integration caps and modified Stokes's kernels are used in spectral geoid determinations of Western Australia.

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Evolution of the river systems of the south-west drainage division, Western Australia

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Abstract

Drainage of the central Yilgarn System is confined within two north-south watersheds, the previously described Central Watershed and the Median Watershed defined here. Runoff today is either intermittent or inactive, but the entire system is gathered to a single outlet through the Median Watershed where it escapes to the Avon. The shape of the catchment with prevalence of north-south alignments, many directed to south coast rivers, suggests that the System originated with southerly drainage. The System is bounded on the south by a watershed parallel to the south coast which formed in the middle to late Cretaceous by marginal uplift of the craton during separation from Antarctica, causing reversal of drainage. There appears to have been a simultaneous down-warp along the line of the present Yilgarn River, the "Chin-Smith lineament". Before uplift the rivers incised canyons into the rifted margin of the continental platform. Subsequently the margin sagged towards the rift forming the Ravensthorpe Ramp and carrying down the valleys as submarine canyons. Along the western part of the south coast there is a secondary axis of uplift, the Stirling Range Axis, 50 km further south. On the eastern side there is evidence for a palaeoriver, the Woolgangie, which has been truncated by the Lefroy-Cowan System. Drainages to the west coast formed in the Mesozoic bounded inland by the Median Watershed. In the early Cretaceous, uplift was associated with continental separation. An extensive canyon was incised at the edge of the rift and later drowned. High sea level prevailed in the Perth Basin to the Late Cretaceous. Regression then promoted rejuvenation of the rivers. The Brockman, Mortlock North Branch and Avon owe their alignments to the Chittering and Jimperding Metamorphic Belts. In the Late Eocene, marginal uplift of the craton by 150-200 m in a belt 80 km wide brought up the Darling Range and caused diversions of drainage. Headwaters of the two Moore Rivers (north and east branches) were diverted to the south, as was the upper Mortlock (north branch). Further down, the Mortlock was relocated some distance east. The combined Avon and Yilgarn Rivers were diverted north, from a westerly course, to join the Mortlock. The Arthur and Beaufort Rivers were cut off from the Collie catchment and diverted to join the Blackwood. Depth of the palaeochannels here and beneath the Avon-Yilgarn afford proof of Darling Range uplift. Monadnocks in the Darling Range which have also been cited as evidence for uplift have been identified and mapped.

Introduction

Mulcahy & Bettenay (1972) divided the State into six "major drainage divisions", and Bettenay & Mulcahy (1972) gave a more comprehensive description of valley form and surface features of the South-West Drainage Division. This included centrally the catchment of the Avon and its tributaries (their Avon System, here called the Swan-Avon System) and laterally in the south-west some smaller catchments grouped as the West Coast, Blackwood and South Coast Systems (Fig 1). In addition they included a Monger System to the north-west comprising drainages connecting to the Moore River (Fig 2). These authors foreshadowed their intention to produce a series of papers in which the other drainage divisions would be discussed and it is regrettable that they did not appear. The present study deals with the South-West Drainage Division, omitting the Monger System for reasons of space.

Studies of the surface features of the Western Shield have declined in number in the past twenty years, after numerous publications in the 1960s and 1970s, although new topographic and geological information has continued to become available mainly from two sources. First, the latest sheets to appear in the National Topographic Map Series at scales of 1:100 000 and 1:250 000 (NATMAP, Canberra); these are contoured at 50 m intervals and show abundant spot heights, whereas few heights were previously available. They enable a much better understanding of the conformation of river catchments and of the major features of the whole Western Shield which are difficult to appreciate on the ground owing to the general flatness of the country. Secondly, a 1:250 000 series of geological maps has been completed (Geological Survey of Western Australia); these conform to the grid boundaries and sheet names of the topographic series and provide a complementary treatment of surface features.

It is now possible to reassess the drainage systems in the light of accurate mapping (*cf* diagrams in Mulcahy & Bettenay 1972) and to go beyond descriptions of soils and valley forms to consider the past history and evolution of the drainage as has been done by Clarke (1993, 1994) and by Kern & Commander (1993) for the catchments surrounding the playa lakes of L Lefroy, L Cowan and L Yindarlgooda which lie adjacent to the South-West Drainage Division to the east (Fig 1). They were able to draw upon a large body of subsurface data obtained by drilling which showed the location and geological history of palaeochannels. Within the South-West Division, few comparable data are so far available but recently Salama (1997) reported on drilling and sounding in the alluvia of the lower part of the Yilgarn River (as named by Bettenay & Mulcahy 1972) for 135 km from Lake Baandee down to its confluence with the Avon. In recent years there have been other reports on alluvial and lacustrine sediments in palaeodrainages east of the Darling Range (Wilde & Backhouse 1977; Hill & Merrifield 1993; Waterhouse *et al.* 1995), all of which are relevant to the evolution of the drainage. Further unpublished data collected in the course of groundwater exploration are held by the Water and Rivers Commission.

Methods

The necessary detail showing heights above sea level, the location of active watercourses, of intermittent or inactive drainage lines and watersheds, was obtained from the latest maps in the National Topographic Map series, scale 1:250 000 (NATMAP, Canberra). A version of each sheet comprising this detail was reduced to 1:1 000 000 and assembled into a general map of the Drainage Division which after further reduction appears as Fig 1. The standards to which the 1:250 000 topographic sheets have been produced vary quite widely in some cases. While all are contoured, abundant spot heights are usually given in addition on sheets covering the interior but are very few on those for the west and south coasts, e.g. Perth, Pinjarra, Collie, Pemberton-Irwin Inlet and Mt Barker sheets. In these cases 1:100 000 sheets were used. Such detailed heights were required for stream gradients and the watersheds. Other relevant mapping was Beard's (1998) study of the position of the central watershed of the Western Shield which bounds the Drainage Division on the east, the "major continental divide" of Bettenay & Mulcahy (1972). Beard (1998) also plotted the lateral east-west watershed dividing the Swan-Avon and Monger Systems, with a substantial revision. Bettenay & Mulcahy (1972) extended their Avon System far to the north with a hypothetical Ninghan palaeoriver leading south through Lake Moore, whereas this lake has been shown by later authors (Beard 1973; van de Graaf *et al.* 1977) to belong to the Monger System. These watersheds are shown in Fig 1.

Results

General Overview

Fig 1 shows the South-West Drainage Division, excluding the Monger System to the north, and with parts of the Roe, Lefroy and Cowan drainages to the east. The South-West Division is bounded on the east by the central watershed of the Western Shield and on the north by the watershed with the Monger System. Both of these have been mapped and described by Beard (1998). They are situated on broad expanses known as sandplains (Bettenay 1984) which Beard (1998) held to preserve portions of a plateau surface formed by denudation during the Mesozoic prior to the mid-Cretaceous. They are remarkably even and continuous. The central watershed rises gently from a height of 415 m in the south to 495 m at its junction with the Swan-Avon/ Monger watershed which similarly slopes down gently towards the edge of the Yilgarn Craton at 250 m. Heights along the watersheds shown in the figures are derived from spot heights, contours and survey beacons. Internal watersheds include those separating catchments draining to the west coast and the major south coast watershed which is the inland limit of drainages to the southern coastline. In addition this study brings to light a new and important watershed, termed the Median Watershed as it divides the South-West Division roughly in half. It trends NNW-SSE parallel to the west coast and about 200 km inland. Taking a course of NNW it leaves the south coast watershed near Ongerup, and running more or less parallel to the Pingrup River, passes west of Lake Grace, slightly west of Corrigin and to Mt Stirling where it is crossed by the Yilgarn River. North of this gap at Mt Caroline the watershed resumes, passing west of Kellerberrin, between Trayning and Wyalkatchem, east of Lake Wallambin and on to join the Swan-Avon/ Monger watershed. The Median Watershed is remarkably linear and regular in height and is breached at only one place, a relatively narrow gap between the granite inselbergs of Mts Caroline and Stirling. As the name Stirling already appears rather frequently on the map of Western Australia I propose to name this feature the Caroline Gap. In more pluvial times, all drainage from the huge interior catchment of the Yilgarn and its tributary rivers was concentrated here to escape to the Avon River. Otherwise the Median Watershed effectively separates all drainages flowing directly to the west coast from the interior drainages which I propose to name here the Yilgarn System, regarding it as separate from the Avon System as it appears to have had a different origin and history. It is remarkable that the catchments of all the west coast rivers terminate at the Median Watershed while the drainage from the further interior breaks through at a single point. Taking into consideration also that the drainages in the southern half of the Yilgarn System are aligned with rivers on the south side of the south coast watershed, it seems logical to assume some history of drainage reversal.

In the context of the whole Western Shield, the Median Watershed can be seen to represent a bifurcation of the Central Watershed (Fig 2), which in the north is central to the Shield and trends approximately north-south (Beard 1998) but at its junction with the Yilgarn/Monger watershed it swings to the south-east for a long distance (300 km) and then back to the south-west (Fig 1). The Median Watershed can now be seen to be continuous with the watershed between the Yilgarn and Monger Systems and to constitute a bifurcation embracing the Yilgarn System. This adds to the impression that the Yilgarn System was originally directed towards the south coast, not the west. It may be suggested that the shape of the Yilgarn System indicates that it formerly included the upper portions of the Lefroy and Cowan drainages, and has lost them by river capture. In this event the Central Watershed would have continued to the south-east, although there is no trace of a watershed today.

However, Beard (1998) pointed out that a valley south of Woolgangie is aligned to one of the very few gaps in the Central Watershed and that this axis may be continued through the north-south alignment of Lake Johnston to another gap in the watershed between the Lefroy and Cowan drainages and so through Lake Tay and Pyramid Lake, and another gap, to the south coast. It is suggested that this alignment reveals a palaeoriver, to be termed the Woolgangie Palaeoriver.

Description of the Median Watershed

Where it leaves the south coast watershed, the Median Watershed is 339 m above sea level; northward it soon rises to 350 m, and the 400 m contour is crossed west of Lake Chinokup. From here, heights of 350-400 m are maintained and the watershed is crested almost entirely with sandplains. On the Corrigin map sheet a maximum height of 435 m is attained at Traysurin Hill east of Harrismith; thereafter heights are steadily between 350 and 400 m and the association with sandplains is maintained. North of Corrigin beyond Wogerlin Hill (> 350 m) the sandplain has been eroded and becomes a stony plateau with granite outcrops (Beard 1980). On the Kellerberrin map sheet the watershed passes through Pantapin at 350 m but in dissected country where the heights are maintained by granite outcrops. Between Mt Stirling (≈ 365 m) and Mt Caroline (340 m) is the gap where the channel of the Yilgarn River passes, marked with a spot height of 229 m. North of Mt Caroline the watershed is at first only at 300 m, rising rapidly to 336 m and to 350 m west of Kellerberrin. At Jeljelabine Well 8 km further north, there is a col between 300 and 350 m suggesting a possible former drainage outlet to the Mortlock River. Otherwise, from here to the north end of the Median Watershed, heights are between 350 and 400 m. Patches of sandplain reappear and become more or less continuous from 25 km north of Kellerberrin. As argued by Beard (1998), these sandplains are considered to preserve portions of the Mesozoic surface of the plateau, so that the Median Watershed is of considerable antiquity. Erosion has affected the Watershed for as much as 50 km north and south of the Caroline Cap, but otherwise its surface is generally well preserved.

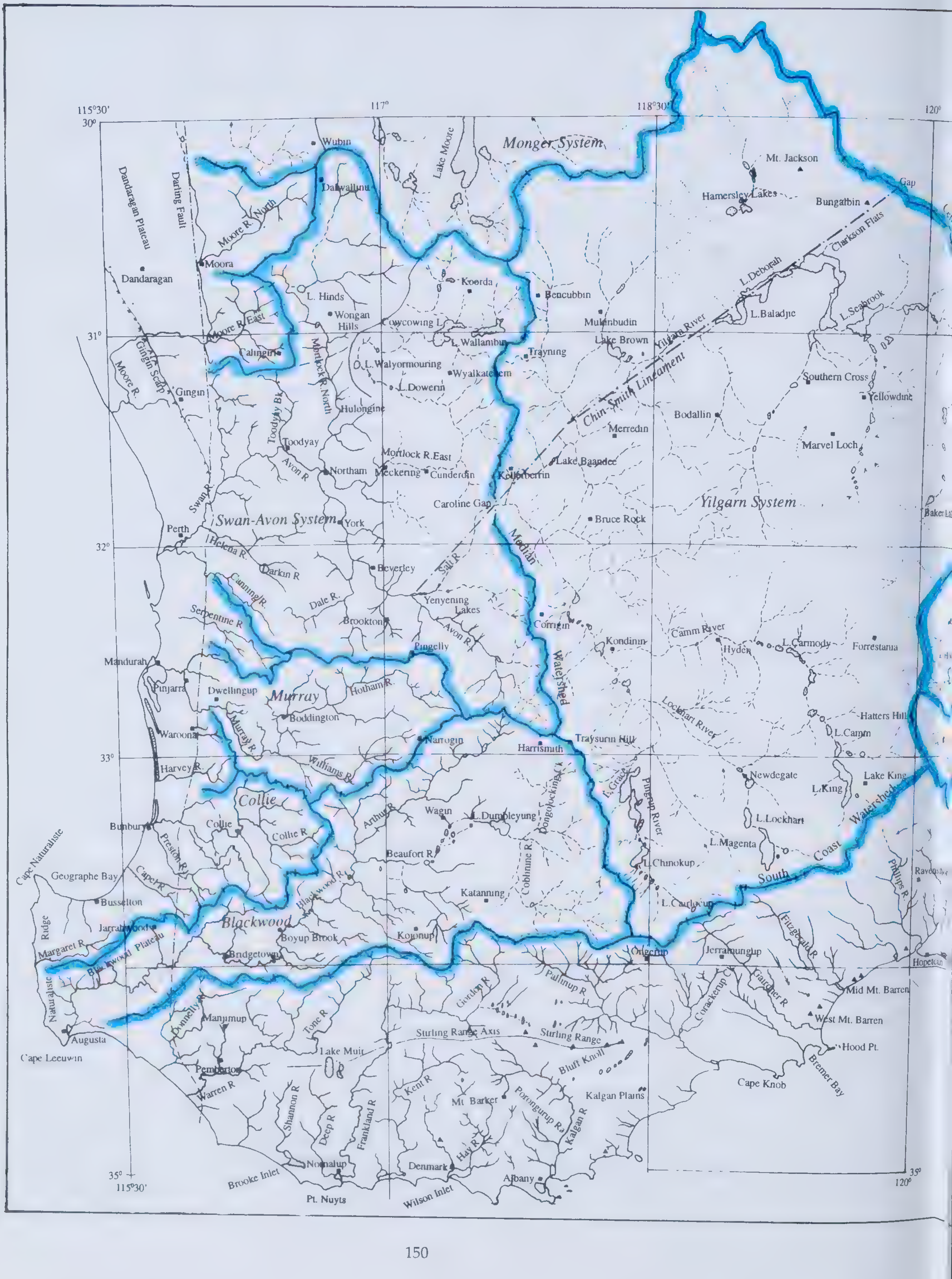
The Swan-Avon System

A sketch profile of the Swan-Avon-Yilgarn Rivers was included by Bettenay & Mulcahy (1972) but a more accurate plot taken from topographic maps is now possible (Fig 3). Heights are from spot heights, contours and bench marks along the way. Length is measured along the valley ignoring minor winding in the case of active watercourses, and directly across playas and salt flats where drainage is intermittent.

The Swan-Avon System falls into several distinct parts. The lowest portion known as the Swan River (reaching the sea at Fremantle; Fig 3) flows across the coastal plain after emerging from the Darling Range at Walyunga, receiving as tributaries the Helena and Canning Rivers which arise in the Range. Above Walyunga the river comes down through the Darling Range in a deeply incised valley on a steep grade, falling 120 m in 62 km (1.93 m km^{-1}). On the coastal plain the grade is only 0.38 m km^{-1}. On its passage through the range, the river receives two tributaries from the north, the Brockman River and the Julimar Brook, with the Toodyay Brook coming in higher up at Toodyay. The Brockman River continues the alignment of the Moore River further north, following the line of the Darling Fault, but has moved a few kilometres to the east of the fault by exploiting the Chittering Metamorphic Belt (Wilde & Low 1978) where some members are more erodible than the common granite.

Above the confluence with the Brockman, the river is known as the Avon because the early settlers on the Swan discovered it independently and did not realise that it was in fact the upper Swan River. The Avon proper rises 200 km to the south-east, near Harrismith, and flows through broadly undulating agricultural country. Between Toodyay and Northam the grade is 0.65 m km^{-1}, above Northam through York and Beverley it is slightly less, averaging 0.52 m km^{-1} as far as the Yenyening Lakes. At Northam, the Avon is joined by the Mortlock River, which actually consists of two separate streams although they are named as the North and East Branches. The North Branch comes down from as far as Dalwallinu while the East Branch has a complicated catchment further inland. The North Branch forms a conspicuous north-south alignment with the Avon and Dale Rivers as they have all exploited the Jimperding Metamorphic Belt (Wilde & Low 1978), forming a distinctive topography of rounded hills that is characteristic of these valleys (see York Vegetation System, Beard 1979). In the far north of the North Branch catchment, there are signs of diversion of drainage where west-trending tributaries are ponded at Lake Hinds and turned to the south instead of continuing west to the Moore River. Further downstream between Goomalling and Bolgart, the Mortlock River runs southward parallel to the Toodyay Brook with about 25 km between them, and the geological map (Wilde & Low 1978) shows this interfluve as a broad area of colluvial deposits. It forms a nearly flat plain scattered with small lakes at a general height of 240-260 m, standing about 50 m above the Mortlock River on the east side. This can be interpreted as an abandoned valley of precursors to the present rivers. The Mortlock River today flows due south in a valley floored with alluvial deposits as far as Hulongine. The grade from Lake Hinds to this point is 0.96 m km^{-1}. From Hulongine down to the confluence with the Avon at Northam, the Mortlock River turns more to the west in a narrower valley, suggesting a steepening of grade, but this is hardly significant, being 1.05 m km^{-1} over this distance.

In the catchment of the East Branch, drainage in the north is first collected in Lake Wallambin and the Cowcowing Lakes with a channel to the west through salt flats and small playas as far as Lake Walyormouring, altitude ≈ 268 m (lake level variable). The grade on this stretch is very low, only 0.23 m km^{-1}. Drainage further to the west is blocked by a north-south ridge running at 320 to 340 m, though there is a gap <300 m south-west of Lake Walyormouring, which may indicate a former outlet to the Mortlock North Branch. Drainage at the present day turns south-east to Lake Dowerin (251 m) where it continues to the south through salt flats and small playas until, between Kellerberrin and Cunderdin, it turns west through Meckering to become the active Mortlock River. On the map this sinuous course appears unlikely, traced only through inactive channels, but the levels and


115°30'
30°
117°
118°30'
120°
31°
32°
33°
35°
Monger System
Mt. Jackson
Hamersley Lakes
Bungalbin
Gap
Clarkson Flats
L. Deborah
L. Baladjie
L. Seabrook
Wubin
Dalwallinu
Lake Moore
Dandaragan Plateau
Darling Fault
Moore R. North
Moora
Dandaragan
Koorda
Bencubbin
L. Hinds
Wongan Hills
Cowcowing L.
Mukinbudin
Moore R. East
L. Wallambin
Lake Brown
Yilgarn River
Calingiri
Trayning
Gingin Scarp
Moore R.
Mortlock R. North
L. Walyormouring
Wyalkatchem
Chin-Smith Lineament
Southern Cross
Yellowdine
Gingin
L. Dowerin
Hulongine
Bodallin
Merredin
Toodyay Bk
Toodyay
Marvel Loch
Mortlock R. East
Avon R
Northam
Meckering
Cunderdin
Kellerberrin
Lake Baandee
Swan R
Caroline Gap
Yilgarn System
Swan-Avon System
York
Bruce Rock
Perth
Helena R
Median
Darkin R
Beverley
Salt R
Canning R
Dale R.
Yenyening Lakes
Serpentine R
Brookton
Avon R
Corrigin
Kondinin
Camm River
Hyden
L. Carmody
Forrestania
Watershed
Mandurah
Pingelly
Pinjarra
Dwellingup
Murray
Hotham R.
Lockhart River
Boddington
Hatters Hill
Murray R
Waroona
Narrogin
Harrismith
Traysurin Hill
L. Camm
33°
Harvey R.
Williams R
L. Grace
Pingrup River
Newdegate
Lake King
L. King
Collie
Dongolocking C
Bunbury
Collie
Collie R
Arthur R
Wagin
L. Dumbleyung
L. Lockhart
Watershed
Cape Naturaliste
Preston R
L. Magenta
Geographe Bay
Beaufort R
Coblinine R.
Capel R
L. Chinokup
Coast
South
Phillips R.
Ravensthorpe
Busselton
Blackwood R
Katanning
L. Carlecatup
Ridge
Jarrahwood
Blackwood
Boyup Brook
Kojonup
Fitzgerald R
Margaret R
Blackwood Plateau
Bridgetown
Ongerup
Jerramungup
Hopetoun
Naturaliste
Pallinup R
Gordon R
Gairdner R
Coracketup C
Mid Mt. Barren
Donnelly R
Manjimup
Tone R
West Mt. Barren
Augusta
Stirling Range Axis
Stirling Range
Hood Pt.
Cape Leeuwin
Lake Muir
Bluff Knoll
Bremer Bay
Pemberton
Cape Knob
Warren R
Kent R
Mt Barker
Porongurup Ra
Kalgan Plains
Shannon R
Deep R
Frankland R
Kalgan R
Hay R
Nornalup
Denmark
35°
115°30'
Brooke Inlet
Albany
120°
Pt. Nuyts
Wilson Inlet

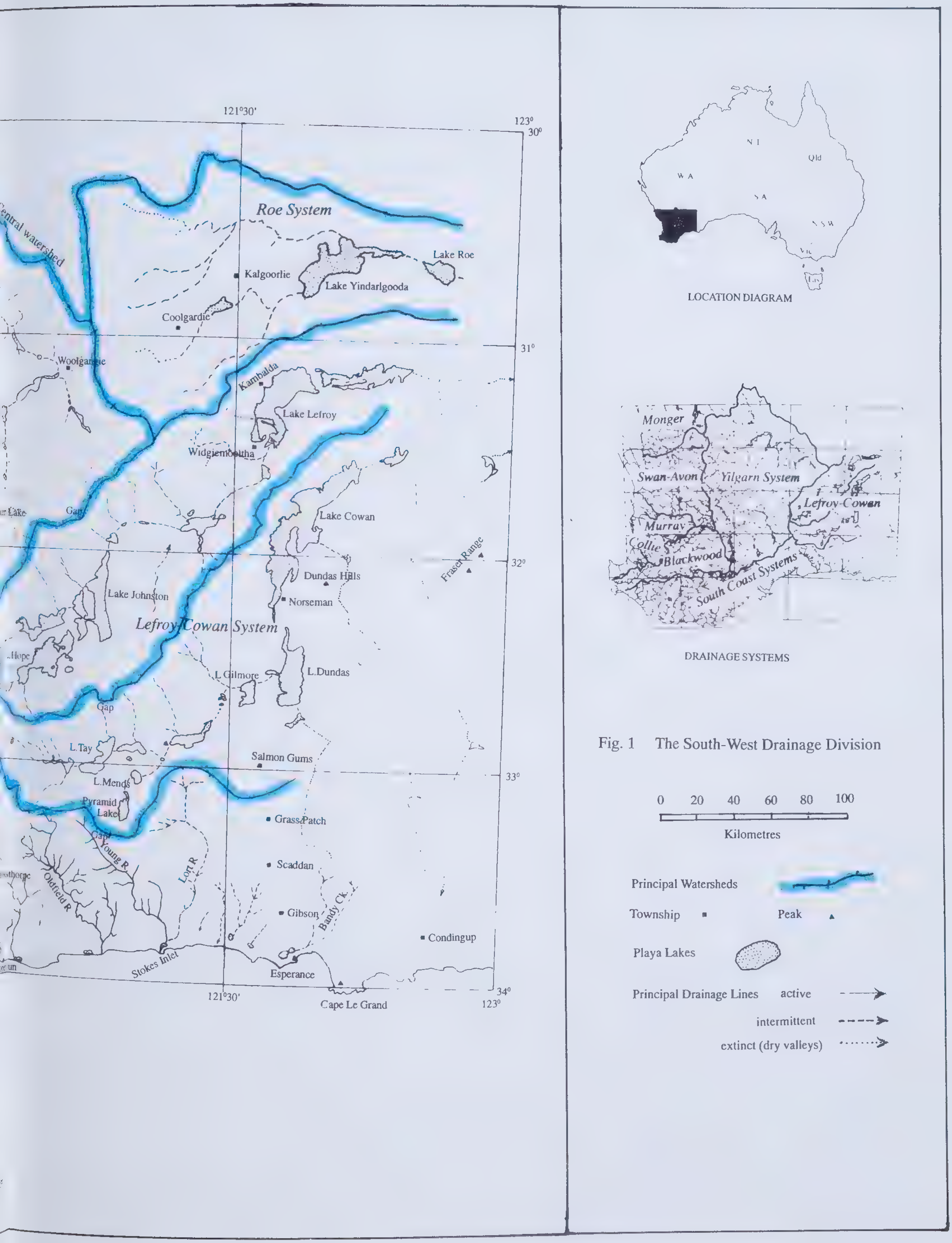


Fig. 1 The South-West Drainage Division

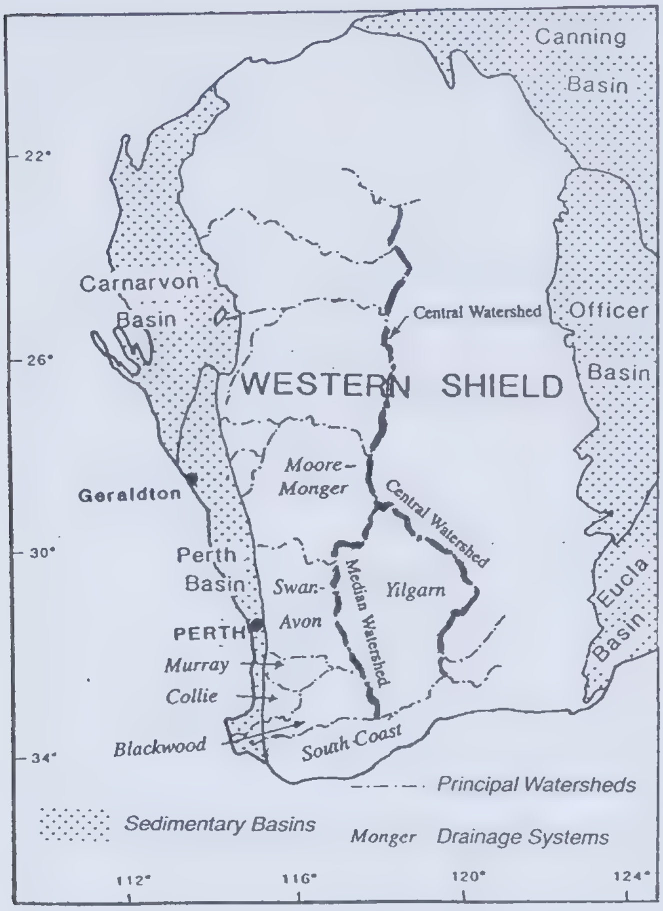


Figure 2. The Western Shield showing the Central Watershed, Median Watershed and other principal watersheds.

mapping of the salt lands prove it to be factual. The average grade from Lake Walyormouring to Meckering is as much as 0.60 m km^{-1}, but after crossing the well-known Meckering Line (Mulcahy 1967) it steepens to 1.28 m km^{-1} to Northam.

At the Yenyening Lakes, 20 km south-east of Beverley, the Avon River is joined by an intermittent channel which in more pluvial times must have brought in the entire run-off from the inland plateau, a huge area extending 300 km to the east and 400 km north to south. This channel comes down 70 km from the Caroline Cap in the Median Watershed, as described above. Salama (1997) showed that this channel, locally called the Salt River, overlies a deeply incised palaeochannel about 70 m deep below the present surface, and relatively narrow. By contrast, the grade of the palaeoriver is only 0.35 m km^{-1}, much the same as the present day and implying sluggish flow. Samples from two boreholes at the Yenyening Lakes were found to be no older than Miocene, contrary to expectation of an Eocene date in keeping with other deposits reported east of the Darling Range by Wilde & Backhouse (1977), Hill & Merrifield (1993) and Waterhouse *et al.* (1995). Salama (1997) accepted the suggestion of Mulcahy *et al.* (1972) that the Avon had formerly flowed over the present Darling Range through the Darkin Swamp and down the course of the Helena River, and considered that a general uplift of the Darling Plateau had ponded drainage in the lower Yilgarn River with formation of a "huge lake" which had eventually drained laterally through the present Avon. This will be discussed later.

The West Coast System

South of the Swan-Avon River there are some small active rivers rising in and draining the Darling Range, principally the Murray and Collie Rivers. The Swan River has two tributaries rising in the Darling Range, the Helena and Canning Rivers, which unite with it on the coastal plain. South of these is the short Serpentine River which peters out on the plain, then the larger Murray River which reaches the sea at Mandurah via the Peel Inlet. The Murray has two tributaries, the North and South Dandalup Rivers, which come down from the Range and join it at Pinjarra. Upstream the Murray River is formed by the union of two tributaries, the Hotham and Williams Rivers, which rise 300 km from the mouth beyond the Darling Range between Pingelly and Narrogin, close to the source of the Avon at an altitude of 350 m. The Hotham and Williams Rivers flow west through undulating agricultural country. On meeting the Darling Range the Hotham turns south just west of Boddington for 20 km to join the Williams River. The combined stream, now the Murray, flows west and north-west in a deeply incised valley, to emerge from the Range 5 km north of Waroona, and thence north to Pinjarra and west to the Peel Inlet. From the watershed at the source of the Hotham, the river descends steeply to the 300 m contour. Then in 105 km to Boddington at 217 m it drops 83 m *i.e.* 0.80 m km^{-1}. Below Boddington to the vicinity of Dwellingup, winding through the Darling Range, it drops 80 m in 108 km, 0.74 m km^{-1}, essentially the same grade. However, measuring from a spot height of 132 m on the river south of Dwellingup, the grade abruptly steepens to 5.3 m km^{-1} falling 112 m in 21 km. Thereafter on the coastal plain the grade is 0.62 m km^{-1}. This situation recalls the Swan River below Toodyay to its emergence onto the plain. The vertical height is about the same but the grade on the Murray is far steeper.

South of the Murray River the much shorter Harvey River rises only 20 km into the Darling Range. Further south lies the catchment of the Collie River which has a total length of 130 km. The relief of the Darling Range dies away towards the south so that the Collie River is not so deeply incised. The river system consists mainly of the east and south branches of the Collie River together with its tributaries, the Bingham and the Harris. The general trend of the whole system is west. The middle course of the Collie River from the 250 m contour down to the town of Collie at about 190 m falls 60 m in 50 km, or 1.2 m km^{-1}. Below Collie, the construction of the Wellington Dam complicates the assessment of grade. However, with the aid of figures supplied by the Water Corporation, it is possible to see that the original grade steepened materially to drop 170 m to the coastal plain, 3.8 m km^{-1}. From the foot of the dam wall to the plain the fall is ≈ 110 m in 20 km, 5.5 m km^{-1}. This steep grade is similar to that on the Murray River, but the total fall is greater over a longer distance. The small short catchments of the Preston and Capel Rivers complete the West Coast System.

The Blackwood System

The Blackwood River has a large catchment of curious shape presenting a number of anomalies apparently due to diversion of drainage. The river is 300 km in length (measured directly from source to mouth) and is formed

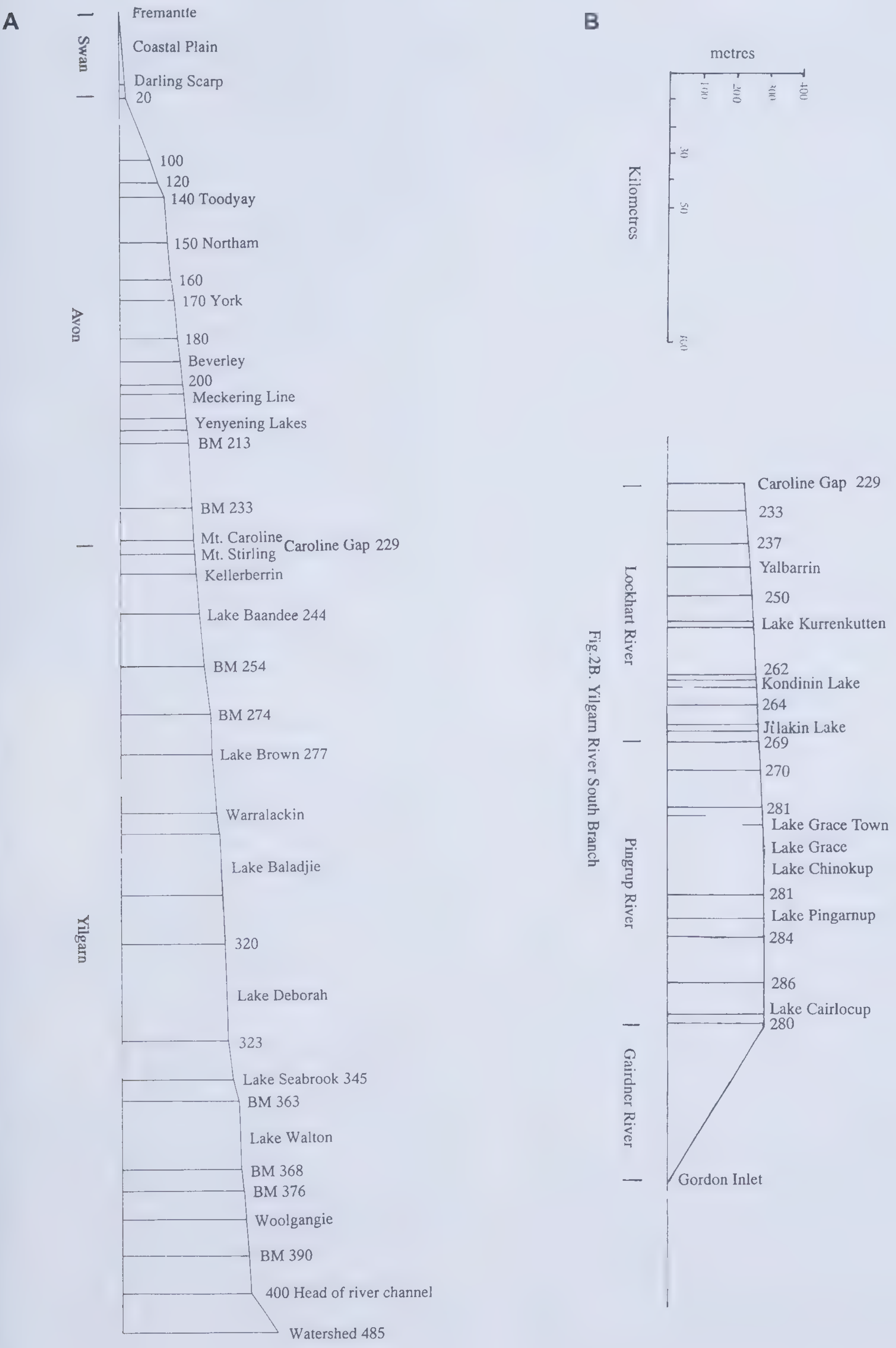


Figure 3. Profile of **A**, the Swan-Avon River and Yilgarn River North Branch; and **B**, the Yilgarn River South Branch.

by the union of two main tributaries, the Arthur and Beaufort Rivers. The Arthur rises near Harrismith in the same area as the sources of the Avon and Murray Rivers and flows south-west through undulating agricultural country on a grade of 0.60 m km^{-1}. There is a well defined watershed of 300-400 m in altitude between it and the Beaufort River, which rises further east where rainfall is lower, the country flatter and drainage intermittent. Two headwater streams, the Coblinine River and the Dongolocking Creek, form a conspicuous north-south alignment though higher up the Coblinine takes a westerly course parallel to the adjacent watershed. This section has a low grade of only 0.17 m km^{-1}. The combined drainage enters Lake Dumbleyung (≈ 257 m, water level variable). This is a permanent salt lake but is said to have been dry before land clearing in the vicinity. Below Lake Dumbleyung to the junction with the Arthur River, the grade is moderately low, 0.50 m km^{-1}, but the prevalence of salt flats and playas is probably due more to lack of water than to low grade. Below the confluence, the Blackwood River proper is permanent, flowing in an extremely sinuous course incised into a relatively narrow valley only 20-40 km wide. Passing Boyup Brook and Bridgetown on a westerly course, the Blackwood eventually crosses the Darling Fault onto the Blackwood Plateau, turning south against the Naturaliste Ridge to meet the sea at Augusta. Owing to the sinuosity of its course it is difficult to measure the length of the river along this section and to estimate grade. Distance along the valley is 220 km giving a grade of 1.0 m km^{-1} but the actual distance along the river's course is probably twice as great, and the grade about 0.50 m km^{-1}.

The recent discovery of Eocene sediments (Waterhouse *et al.* 1995) buried in palaeochannels of the Beaufort and Arthur Rivers in the vicinity of their confluence appears to show that at that epoch drainage was ponded by some epeirogenic movement, escaping as the modern channel of the Blackwood was formed. This evidence is considered below with that of Salama (1997) in the Avon System.

The South Coast System

The South Coast System consists of a large number of relatively short rivers flowing to the south from a continuous watershed only 60 to 120 km inland, but stretching 650 km from Cape Leeuwin to Salmon Gums (Fig 1). Further east the country is both drier and flatter and the watershed ceases to be traceable. Cope (1975) attributed the formation of this watershed to a line of uplift called the Jarrahwood Axis, named after a small settlement on the Blackwood Plateau. It will be seen from Fig 1 however that the watershed on which Jarrahwood is situated is actually the northern watershed of the Blackwood catchment formed (as will be shown later) by an uplift of the Darling Range. At the southern extremity of this uplift, the watershed continues to the north-east and is unrelated to the South Coast Watershed marking the other side of the Blackwood catchment. It is suggested here that the name Jarrahwood Axis is not correctly applicable to the latter. Cope (1975) regarded it as a hinge line formed in the course of separation of Australia from Antarctica in the Early Tertiary. To the south the Darling Plateau sagged towards the rift, forming a slope called the Ravensthorpe Ramp which extends off-shore to the edge of the continental shelf. On-shore, the rivers of the South Coast System have developed. Cope(1975) essentially regarded the Axis as a hinge line along which the surface of the stable Darling Plateau took on a southerly slope, rather than as a line of epeirogenic uplift. He noted that his data appeared to show a "slight reversal of dip" to the north of the axis, but information available at the time was insufficient to confirm this. The South Coast Watershed appears, at the western end where it divides the Blackwood from the Donnelly, Warren, Tone and Frankland Rivers, as an inconspicuous ridge with heights of 300 to 350 m. Along this stretch there are no obvious signs of gaps in the watershed or north-south drainage alignments to suggest former channels across it. However Wilde & Backhouse (1977) reported a small Eocene fossiliferous deposit on the crest of this watershed 26 km west-south-west of Kojonup. South and east of Kojonup, maximum heights on the watershed rise to just under 400 m. South of Katanning and as far as Ongerup, the watershed lies on a broad plain at 300-350 m asl which breaks abruptly on the southern edge to headwaters of the Gordon and Pallinup Rivers. From Ongerup east to the junction with the Central Watershed, there is again a broad plain often with small salt lakes and with less of an abrupt fall on the south. Heights of 380 m occur locally but are generally below 350 m or as low as 300 m. Low levels occur at the cols on alignments between the Pingrup and Gairdner Rivers (spot height of 289 m), between the Lockhart and Fitzgerald Rivers (< 300 m by contours) and between the Camm and Phillips Rivers (< 350 m contour). Grades along the watershed are rather low on either side of these cols whose position is chiefly indicated by the drainage alignments. We have no data on possible palaeochannels. East of the junction with the Central Watershed at 415 m, the actual South Coast Watershed and Cope's Jarrahwood Axis separate. The latter is expressed by a well-marked continuous ridge running to the north-east whose heights vary from 344 to 441 m. A col at about 350 m is situated due south of the long axis of East Lake Johnston. Further to the north-east this ridge passes between Lakes Lefroy and Cowan. Lake Lefroy itself is at 295 m and spot heights of 380-390 m are common on the watershed which ends where the eastward alignments of the two lakes come together.

The South Coast Watershed proper continues in a general easterly direction from the junction with the Central Watershed declining in height from 415 m to 330 m north of the Oldfield River and to 250 m at a col south-east of Pyramid Lake. Curving round the headwaters of the Lort River, the watershed is on a flat plain at about 250 m. Further to the east it becomes impossible to trace any actual watershed as there are no drainage channels at the present day and the country becomes lower and flatter. There are two north-south alignments of small playas divided by transverse sand dunes which may indicate the presence of palaeochannels.

The Ravensthorpe Ramp (Cope 1975) is well named since it is along the stretch from Jerramungup to Ravensthorpe that it is steepest and most conspicuous. The Gairdner River here has a grade of 3.0 m km^{-1} (Fig 3B). East of Esperance, drainage becomes inactive and it is no longer possible to trace any watershed. In the western sector where country south of the watershed is at its widest, drainage is complicated by a second axis, parallel and 50 km further south (Fig 1). This was reported but not named by Muhling *et al.* (1985). I term this the Stirling Range Axis as it passes along the line of the Range (maximum height 1060 m) at its eastern end and is prolonged to the west as an inconspicuous watershed at 250-300 m. The Gordon River takes a westerly course north of the Axis for 50 km before breaking through to become the Frankland River. Still further west, the Axis is responsible for the plateau carrying Lake Muir and associated swamps (altitude 170 m). The Stirling Range is formed of Proterozoic sedimentary rocks interpreted as uplifted in the Cainozoic along faults (Myers 1990a). The present study indicates that at least two phases of uplift must be considered, an earlier uplift after which dissection of the Range and formation of Chester Pass and Red Gum Pass took place, and a later and lesser uplift in which drainage through the passes was broken off. The highest point in both today is at 310 m whereas the plain on the north side of the Range is at about 230 m. The difference is too great to be due to valley fill. Uplift of the Range has diverted the Gordon River to the west and the Pallinup to the east, and created a flat plain between their headwaters which has no external drainage at the present day and is strewn with small salt lakes. While the Pallinup River escapes to the sea today by joining the Corackerup Creek, there are signs that at first it may have had an outlet around the eastern end of the Range to the Kalgan River, as indicated by a chain of salt lakes which stand at 120 m, well below the level of the Kalgan Plains to the south of them.

The Yilgarn System

The Yilgarn System embraces all the drainage of the interior plateau, focussed to escape at one point through the Caroline Gap. Little flow takes place today except in years of exceptionally high rainfall when the channels are known to flush out in whole or in part. All the drainage is therefore mapped as intermittent or inactive, the latter being dry valleys in the far east and north-east. The System divides naturally into north and south parts, whose courses are united just above the Caroline Cap. The north branch was named the Yilgarn River by Bettenay & Mulcahy (1972); the south branch has three main components which they named the Pingrup, Lockhart and Camm Rivers. These names are conserved here. Fig 3A shows the profile of the Yilgarn River from the Avon confluence along its main channel through Lakes Brown, Baladjie, Deborah, Seabrook and others to the Central Watershed east of Woolgangie, a distance of 525 km. Fig 3B shows the south branch from the Caroline Gap by the Lockhart and Pingrup Rivers to the col marking the head at Lake Cairlocup, and thence down the south-flowing Gairdner River to the sea. The Yilgarn River drops 200 m in 525 km from the head of channel to the Avon confluence (Fig 3A), a grade of 0.38 m km^{-1} which is similar to the 0.35 m km^{-1} calculated by Salama (1997) for the distance below Lake Baandee. The descent is not entirely even since valley fill is locally unequal, and where playas are formed these are more or less level followed by a drop to the next one; however, the overall slope is reasonably uniform and is adequate for discharge during years of high rainfall.

Grades on the south branches (Pingrup, Lockhart and Camm Rivers) are very low. Along the Lockhart section (Fig 3B) in 170 km the fall is 41 m (0.24 m km^{-1}) and along the Pingrup section in 135 km it is only 5 m, virtually level. This stretch includes the lengthy playas of Lake Grace and Lake Chinokup which extend for 50 km. The highest point in this alignment is at 286 m asl in a gap in the South Coast Watershed, beyond which the Gairdner River takes a course south to the sea, falling 286 m in 95 km, a grade of 3.0 m km^{-1}. The upper Lockhart and Camm Rivers show a similar conformation with extensive playas and lead also to gaps in the South Coast Watershed in alignment with the Fitzgerald and Phillips Rivers. The low grade in the upper reaches of all these makes it unlikely that any significant discharge takes place.

Cope (1975) was uncertain whether his Jarrahwood Axis forming the South Coast Watershed was merely a hinge line at the top of the Ravensthorpe Ramp or was accompanied by uplift. We can be tolerably certain that where the Axis abuts the Yilgarn System there was prior drainage across it, but we do not know whether this flowed north or south. This gives four alternatives, based on uplift or no uplift, north or south drainage. With no uplift and northward drainage, there is no reason for the extremely low grades in the upper courses of the Pingrup, Lockhart and Camm Rivers. With uplift and northward drainage, there is even less reason for this; grades would have steepened. With no uplift and southward drainage, the rivers would have continued to flow south across the Jarrahwood Axis and deepened their beds. With uplift and southward drainage, the rivers north of the Axis were reversed and conform to the profile in Fig 3B. This last alternative is therefore preferred.

It is assumed from the general shape of the Yilgarn System and the prevalence of north-south alignments (more precisely, NNW-SSE at right angles to the south coast, or possibly structurally controlled by the trend of the greenstone belts), that the entire System originally flowed south into Antarctica. After reversal along the south coast axis, a new outlet was developed at the Caroline Gap. It is possible that this particular point was determined by a down-warp simultaneously with the elevation in the south and parallel to that axis. This is not unlikely or impossible since tectonic movements in the south of the Yilgarn Craton were contemporary with a very major event, the separation from Antarctica. In the geological survey of the Jackson area, Chin & Smith (1983) drew attention to a "major lineament" which trends WSW across the southern part of the Jackson map sheet, controlling the major drainage. It runs from the Clarkson Flats ENE of Lake Deborah, through Lake Deborah West and Lake Baladjie. Beard (1998) showed that still further to the east it is aligned to a gap in the Central Watershed. It is apparent from Fig 1 that if extended to the WSW the lineament passes through the Caroline Gap and on towards the Yenyening Lakes. The whole main channel of the Yilgarn River below Lake Deborah conforms approximately to this lineament. It could be due to coincidence but is certainly suggestive. Chin & Smith (1983) showed that the lineament is parallel to a Proterozoic dyke suite that transects all Archaean lithological boundaries, "suggesting that it is related to the fracture system which controlled the dykes". It may be felt that a feature of Proterozoic origin is unlikely to be controlling Tertiary palaeodrainage, but perhaps this lineament represents a line of crustal weakness which was exploited by Phanerozoic epeirogeny. I propose that it be named the Chin-Smith lineament.

Discussion

The Lefroy-Cowan and Roe Systems

Some discussion of the drainage systems further east of the South-West Division (Fig 1) is relevant as these have been previously studied, the Roe Palaeodrainage by Kern & Commander (1993) and the Lefroy and Cowan Palaeodrainages by Clarke (1993, 1994). The development of these has been primarily controlled by tectonic movements in the Eucla Basin. In Clarke's view, drainages developed initially towards the north and were deflected more and more to the east as the Eucla Basin subsided. The Cowan palaeoriver in particular flowed north from the direction of Antarctica. This situation remained stable until major subsidence in the Eucla Basin in the Middle Eocene brought about the Tortachilla transgression where the valleys were flooded and sediments deposited. Significant differences between deposits in Lake Lefroy and Lake Cowan show that they were not connected at this stage, Lake Cowan being open to the sea on the south. Clarke (1994) thought that the Cowan drainage had been reversed to the south by the uplift of the"Jarrahwood Axis" represented by the present watershed between the Lefroy and Cowan drainages. Clarke preferred to date this to the Jurassic instead of the Eocene as proposed by Cope (1975), but this must be considered too early. It seems far more likely that the drainage reversal took place at the time of separation of Australia from Antarctica, beginning in the Eocene. In the Late Eocene, an even more extensive transgression, the Aldinga, took place with renewed flooding of the valleys and sedimentation. The term Aldinga has since been changed to Tuketja (Clarke *et al.* 1996). This episode implies still greater subsidence of the Eucla Basin and adjacent land areas with steepening of grade by the rivers so that Lake Cowan was captured by the Lefroy. Lakes Tay, Mends and Dundas continued to be connected to the sea on the south. By the Miocene, flow through the system more or less ceased largely because uplift of the Eucla Basin and adjacent land reduced grades. At the present day, Lake Cowan at 260 m is higher than Lake Dundas (241-244 m), from which a southward palaeochannel can be deduced through country of the same altitude for some 40 km until it descends towards the coast at Esperance. Lake Gilmore at about 240 m belongs with Lake Dundas but the lakes to the WSW should not be shown (as by Clarke 1994) as connected to these as they are lower (Lake Tay 236 m, Lake Mends < 240 m, Pyramid Lake 237 m) showing original drainage to the south. The final elevation of the Eucla Basin has left these lakes on a plateau which is still undissected by the Lort, Young and Olfield Rivers, and where there is very little fall, if any, from one lake to another. Sediments dated as Miocene-Pliocene in Lake Tay (Bint 1981) can be attributed to the rejuvenation of these lakes on their plateau situation during a later pluvial interval.

The history of the Roe Palaeodrainage further north described by Kern & Commander (1993) is similar except that the only evidence of marine sedimentation is well downstream, 180 km east of Kalgoorlie. The valley-fill deposits in the upper catchment are fluvial and lacustrine, and exclusively of Late Eocene age.

The Yilgarn and South Coast Systems

As with the Lefroy-Cowan System, the historical development of the Yilgarn and South Coast Systems has been strongly affected by the separation of Australia from Antarctica and associated movements in the Eucla Basin. The interpretation given here is largely based on Middleton (1991). Separation from Antarctica began in the Jurassic with formation of a transcurrent fault situated along the present southern edge of the continental shelf. Subsidence occurred locally in two places forming the Albany and Eyre sub-basins with half-grabens which became covered with Jurassic sediments. The rift so formed gradually widened. Drainage from the north poured over the edge of the continental platform incising canyons. As the rift widened to form a seaway by the Late Neocomian, the edge of the plateau slumped towards the rift carrying down the canyons below sea level. This is the origin of the numerous submarine

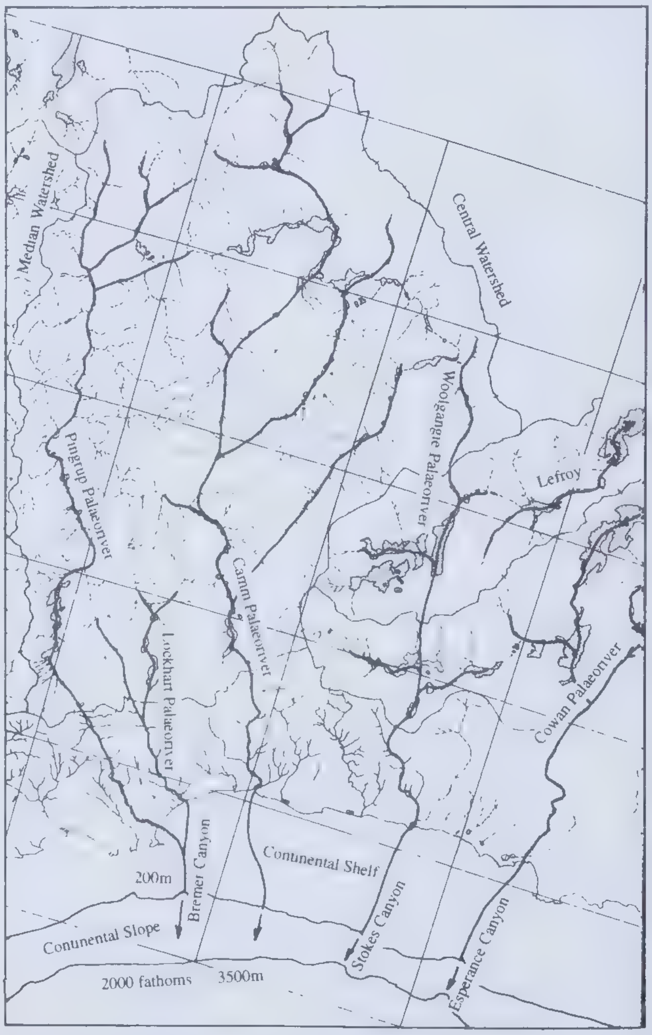


Figure 4. Palaeodrainage of the Yilgarn, Lefroy and Cowan Systems, epoch Late Cretaceous (bold lines) with probable connection to submarine canyons.

canyons along this coast mapped by von der Borch (1968) who also later described this mode of formation (von der Borch *et al.* 1970). The existence of such canyons has been difficult to explain and might usefully form the subject for another paper dealing specifically with the south and west coasts of Western Australia.

The palaeodrainage at this epoch, Late Neocomian, with south-flowing rivers directed to the edge of the continental shelf which was then the shoreline, is shown in Fig 4 with hypothetical connections to the three major canyons named by von der Borch (1968). The south-flowing Woolgangie Palaeoriver is included in this diagram as part of the Yilgarn System and is connected to the Stokes Canyon. Further east, the Cowan Palaeoriver, flowing south at that time, is shown connected to the substantial Esperance Canyon. It is suggested that the middle course of the Woolgangie Palaeoriver now represented by the Johnston Lakes, was captured at some time by the Lefroy drainage. The group of Lake Tay, Lake Mends *etc.* is believed always to have been separate from the Cowan drainage.

The sagging of the continental margin created the Ravensthorpe Ramp, sloping down to the south from a hinge line at plateau level to the edge of the continental shelf. This movement also generated a slight uplift along the axis and a slight downwarp along the Chin-Smith lineament, reversing drainage in the southern half of the Yilgarn System, to find a new outlet at the Caroline Gap. The relative movements involved are not great. The cols at the upper end of the Pingrup, Lockhart and Camm Rivers are at 289, 300 and 300-350 m and probably do not contain any appreciable depth of valley fill. The course of the Yilgarn River along the Chin-Smith lineament descends from 320 m at Lake Deborah to 229 m at the Caroline Gap but there is substantial valley fill, say an average of 50 m, so that the basement descends from 270 to 180 m. The difference in level is not great but sufficient to enable reverse flow in the drainage. Without some depression along the Chin-Smith lineament it would appear that uplift along the South Coast Watershed could not have reversed drainage effectively, unless the South Coast Watershed was originally uplifted more and has since partly subsided. Low grades at the source of southern rivers may support this supposition.

Sea floor spreading between Australia and Antarctica halted in the mid-Aptian, to be renewed in the Eocene (Middleton 1991). It is probable that the formation of the Ravensthorpe Ramp was a gradual process, which cannot be precisely dated, taking place in the Cretaceous. It had been formed by the Middle Eocene when sediments of the Plantagenet Group were deposited upon it. Renewal of the sea floor spreading was accompanied by major subsidence in the Eucla Basin so that the Lefroy-Cowan drainages were flooded and the sea invaded the Ravensthorpe Ramp. It seems probable that the whole southern edge of the Yilgarn Craton was tilted down to the east at this time, since the transgression was widest in the east. West of the Lefroy-Cowan area there is no evidence for a general Eocene transgression inland although it has been suggested by various authors (*e.g.* Wilde & Backhouse, 1977) when they reported thin sediments dated as Eocene from two localities near Kojonup at altitudes of 310 and 320 m, close to the south coast watershed and on its north side. However these can be regarded as of fluviatile origin.

Evidence for the dating of the drainage reversal in the south of the Yilgarn System can be deduced from Salama (1997). When discussing the sequence of events in the West Coast Systems (see below) it will be shown that the data indicate that the Yilgarn River must at one time have flowed directly west across what is now the Darling Range. At some stage, concluded to have been in the Late Eocene, an uplift of the Darling Range plateau ponded the river into a huge lake which found a new outlet down the Avon from Beverley to Toodyay. The Yilgarn River must have established its channel through the Caroline Gap prior to the Late Eocene and quite some time before since a deep gorge was excavated. The tectonic movements on the inland plateau and the reversal of drainage must also have taken place well before the Late Eocene, probably in the Cretaceous. This is in accord with the evidence from the south coast. Cope (1975) proposed an Eocene date for the formation of the Jarrahwood Axis and the Ravensthorpe Ramp. Clarke (1994) objected to this as being too late, and preferred the Jurassic. This on the other hand is manifestly too early since it cannot precede rifting between Australia and Antarctica. A Middle to Late Cretaceous date would seem to be a necessary compromise.

The West Coast Drainage Systems

Just as the separation from Antarctica and associated epeirogeny were crucial to development of the south coast systems, the contemporaneous separation from land to the west and tectonic movements in the Perth Basin have affected the drainage to the west. The treatment here follows the description given in Cockbain (1990). The river systems of the Yilgarn Craton are believed to have originated in or before the Jurassic (Beard 1973; van de Graaf *et al.* 1977; Clarke 1994). Triassic and Jurassic sandstones deposited thickly in the Perth Basin demonstrate erosive activity on shore. In the Early Cretaceous there was uplift coincident with the beginning of continental separation on the west, and the rivers pouring over the edge of the rift formed a large and complex canyon which with later sagging of the continental margin has become the submarine canyon of today west of Fremantle (von der Borch 1968). This canyon has at least four branches, probably receiving drainage concentrated here from all this part of the coast, since no other has been located.

During the Neocomian as the continental margin sank again, the sea re-entered and rivers discharged into shallow marine waters. Valley-fill deposits such as the Bullsbrook Formation (non-marine) were laid down in valleys cut into the Darling Scarp. After a brief regression in the Aptian, high sea level was established for the remainder of the Cretaceous and the rivers discharged into deep water. There is no similar evidence for high sea level on the south coast at this time. In the Perth Basin, sedimentation continued but at a slower rate. Sandstones were thinner and accompanied by carbonates. This seems to show diminution of erosion on shore which could be due to reduction of grade in the rivers resulting from levelling of the land surface and/or the development of a denser and more widespread plant cover following the diffusion of the angiosperms in the Albian-Aptian as

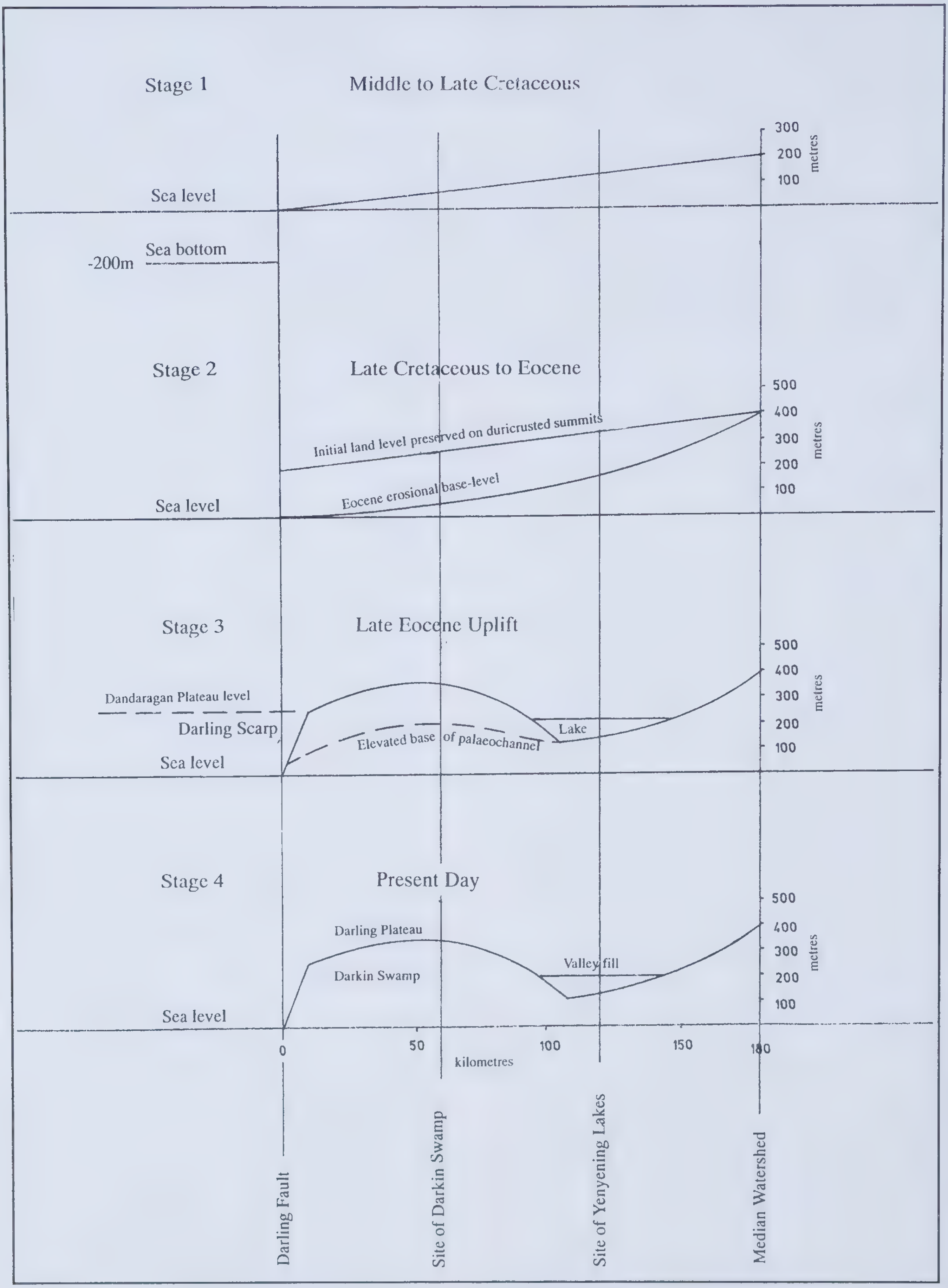


Figure 5. Scale diagrams showing development of drainage in the Swan-Avon System.

suggested by Beard (1989). In the later Cretaceous after deposition of the Poison Hill Greensand, marine transgression of the Perth Basin began to recede, exposing the sea floor (Playford *et al.* 1976). However this surface was evidently not far above sea level. The Dandaragan Plateau appears to have been exposed but the Victoria Plateau further north was still receiving thin deposits into the Eocene. It is difficult or impossible in these cases to say whether withdrawal of the sea was due to fall in sea level *per se* or to uplift of the land. In either case the practical effect is an uplift above sea level. Withdrawal of the sea at the time and place under discussion would have resulted in a relative uplift by an amount equal to the depth of water offshore when the Poison Hill Greensand was being deposited. As open marine conditions prevailed, a depth of 200 m should be allowed (A E Cockbain, pers comm). The sequence of these events in the Perth Basin is shown diagrammatically in Fig 5. Stage 1 represents the situation during the high sea level of the Cretaceous along a section drawn from the Darling Fault at Midland to the Median Watershed at Corrigin passing through the Darkin Swamp and the Yenyening Lakes which are thought to have lain on the ancestral Avon River. At the epoch of Stage 1 the formation of the Mesozoic surface of the Yilgarn Plateau is held to have been completed (Beard 1998), sloping gently down to the coast from the Median Watershed and drained by sluggish rivers in shallow valleys. The grades and levels were in accord with the high sea level of that time, with the shore line initially along the Darling Fault but gradually moved a few kilometres east of it by marine erosion. At this stage a height of 200 m for the Median Watershed has been assumed as it is in accord with later evidence.

Recession of sea level at the end of the Cretaceous had the effect of raising the river mouths along the Darling Fault, discharging onto a plain below. This level is represented today by the Dandaragan Plateau (after further uplift later). With the river mouths initially > 200 m above sea level and rainfall high in the Late Cretaceous and Early Tertiary, it is likely that the rivers lowered their beds to the new base level and that the valleys were adjusted accordingly throughout the catchments. A period of thirty million years from the Maastrichtian to the Upper Eocene is available for this process, arriving at Stage 2 in Fig 5. Lowering of sea level by 200 m has had the effect of raising the Median Watershed to 400 m, roughly its present height, maximum 385 m near Corrigin. As this watershed is capped by duricrust and sandplain deposits it is thought not to have been disturbed since the Eocene. A tributary of the Avon comes down to join the confluence of the Avon and Yilgarn Rivers at the present site of the Yenyening Lakes where the palaeochannel had been excavated to 140 m asl (Salama 1997). Numerous authors (*e.g.* Mulcahy *et al.* 1972; Salama 1994, 1997) have suggested that the combined Avon-Yilgarn flowed directly west from there passing through the present site of the Darkin Swamp. This swamp today lies in a valley system on the Darling Plateau and at the epoch of Stage 2 the river must have incised a substantial valley about 200 m deep below the plateau level, as is the situation today. The river level is shown on the diagram with the base of the valley at the Darkin Swamp estimated at about 50 m asl.

At this same Late Cretaceous stage, rejuvenation of the rivers with increased vigour of stream flow and volume of sediment, augmented by the reversal of drainage inland and the formation of the Caroline Gap, at first excavated a substantial valley west of the Darling Fault which in late Palaeocene-Early Eocene time became filled with siliciclastics (the King's Park Formation) after a further marine transgression (Cockbain 1990). This implies that the former sea floor exposed by the Late Cretaceous regression stood at a high enough level for the incision, at least near shore. Further offshore, excavation could have been taken deeper by turbidity currents and joined to the pre-existing submarine canyon. This process is known to be possible where only soft sediments are being removed (Kuenen 1953; Conolly 1968). In Late Palaeocene time, some subsidence or transgression is required for the deposition of the King's Park Formation in the near shore part of the canyon as the sediments are 265 m thick in the type section below King's Park and thicker off shore.

The levels involved create some difficulty for this interpretation. The valley in which the King's Park Formation was deposited must have been incised into a southward continuation of the Dandaragan Plateau, a feature now missing from this part of the Perth Basin. The plateau now stands at 250-300 m asl whereas the top of the King's Park Formation is at sea level. It seems evident that after incision of the valley and before its filling with sediment some considerable subsidence of this part of the Perth Basin took place. Absence of the continuation of the Dandaragan Plateau to the south was formerly explained by marine erosion (Playford *et al.* 1976) but is now seen to be due to subsidence of a syncline, the Swan Syncline (Davidson 1995) which carried down the Jurassic and Cretaceous sediments in the Basin south and west of the present Gingin Scarp, leaving the Dandaragan Plateau intact further north. The axis of the syncline trends NNE-SSW, situated some 15 km west of the Darling Fault at Perth, approaching it in a northerly direction. No movement along the Fault itself is implied, the syncline being treated as slumped against the Darling Scarp. The next event to affect the situation (Stage 3 in Fig 5) was epeirogenic uplift of the western margin of the Yilgarn Craton during the later Eocene. Since this was synchronous with down-warp of the Eucla Basin and adjacent land, it might be suggested that there was a general tilt of the Craton. The evidence from the west coast however requires a differential uplift. Salama (1997) reported that the Yilgarn River had been obstructed by an uplift of the Darling Range to the west, causing the formation of a "huge lake" centred on the Yenyening Lakes where up to 70 m of sediment were deposited. The river could not have continued to the west because the base of the palaeochannel at the Darkin Swamp is now 60 m above the base at the Yenyening Lakes, implying uplift by more than that amount. The Yilgarn River could not at first escape to the north down the present course of the Avon since the base of the river channel at Beverley, York and Northam is also higher than the Yenyening Lakes, so that some ponding would have taken place. Since the Darkin Swamp was originally downstream and therefore lower than the Yenyening Lakes palaeochannel, the evidence calls for an uplift of 140 m. Diversion of drainage in the extreme north of the

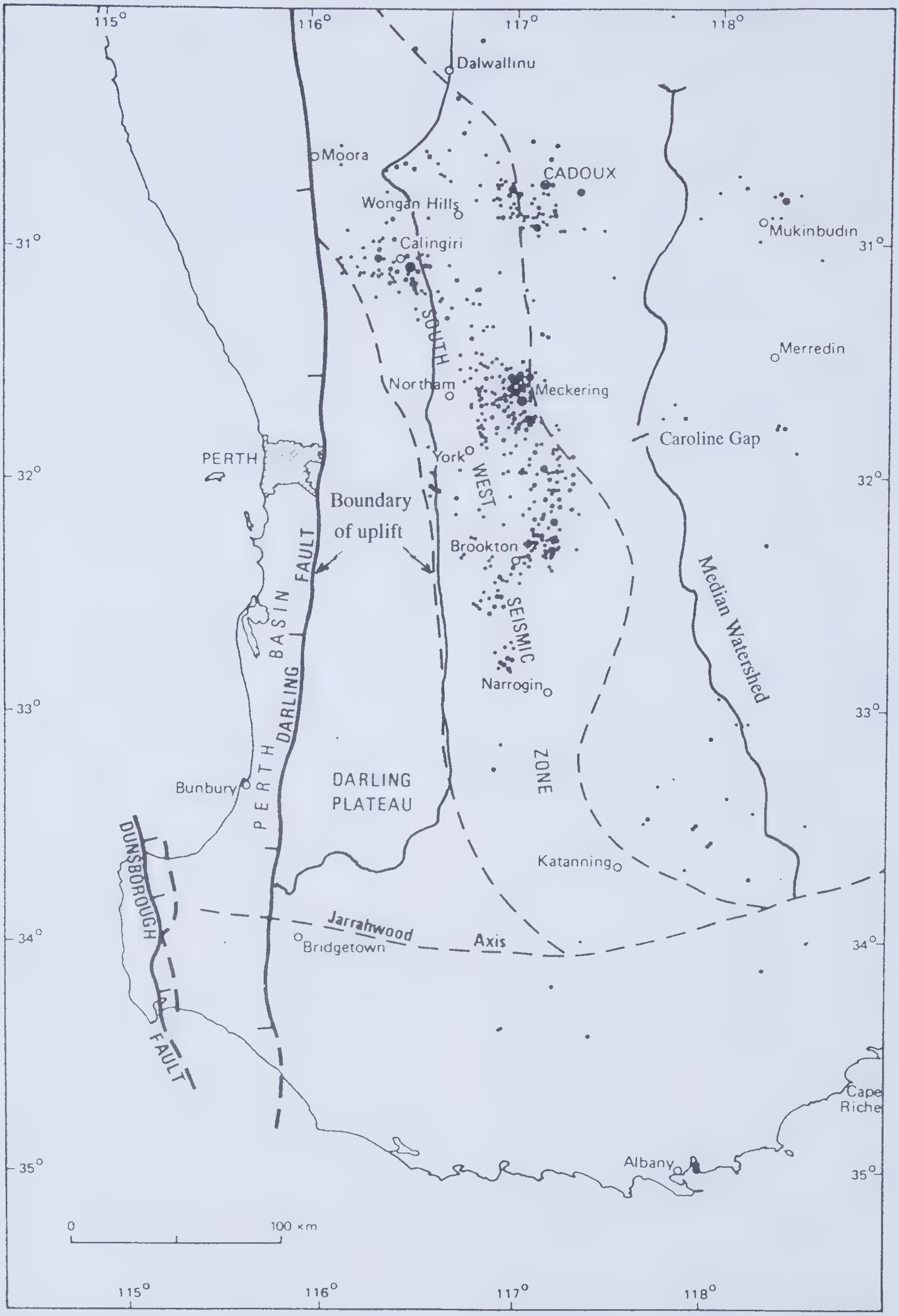


Figure 6. The South-West Seismic Zone (after Lewis *et al.* 1981) contrasted with the Median Watershed and the Darling Plateau uplift.

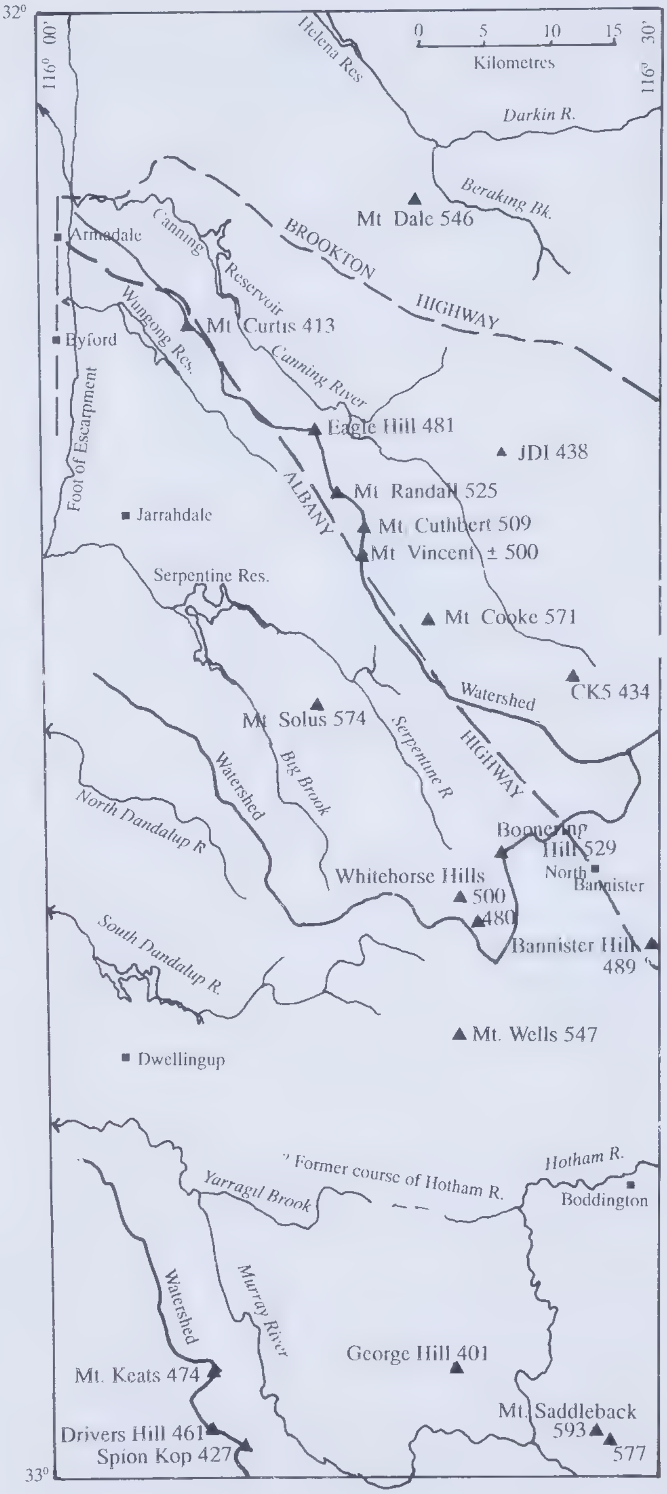
Mortlock catchment indicates uplift of 50-100 m. Palaeochannels in the Beaufort River system indicate uplift to the west of >110 m.

Marginal uplift on the west of the Yilgarn Craton is not a new idea and goes back at least to Jutson (1914) though it seems to have been generally overlooked in recent years. It was taken up by Mulcahy *et al.* (1972) as central to their conclusions on landforms and soils "on an uplifted peneplain in the Darling Range". They showed that the Range is a zone of some 80 km in width of greater elevation than country to the east, which was taken to imply a marginal upwarping of the Craton.

It is not clear how this uplift relates to that postulated by Libby & de Laeter (1979) and de Laeter & Libby (1993) from biotite dates along two traverses across the Darling Range in the central area near Perth, since it is dated as Silurian. The very considerable uplift calculated is likely to have been eroded away by the end of the Cretaceous, especially as the glacial episode of the Early Permian intervened. Effects on evolution of the drainage call for a renewed uplift in the Early Tertiary. For dating of this we can rely on the macrofossil and palynological data derived from fluviatile sediments apparently laid down in the early stages of disruption of drainage by the uplift, These show Late Eocene to Oligocene in one case, Middle Eocene to Oligocene in another (Hill & Merrifield 1993), Eocene (Wilde & Backhouse 1977) and possibly late Middle to Late Eocene (Waterhouse *et al.* 1995). All these agree sufficiently closely to suggest a Late Eocene date. Only the results from Salama (1997) are at variance with this. Material from two boreholes at the Yenyening Lakes was dated as no earlier than Miocene and must have been deposited in a much later stage of valley fill, although found at a considerable depth, 56-57 m and 63-68 m.

It is worth considering, as an alternative explanation, whether the disruptions of drainage may have been due to movements in the South West Seismic Zone (Fig 6). Everingham (1968) and later authors (Gaull *et al.* 1990; Doyle 1971; Lewis *et al.* 1981) identified a seismically active zone in the south-west of Western Australia in which several destructive earthquakes have taken place in recent years. This area has been assumed to "fall largely within a down-warped zone which separates the low-relief, gently warped interior of the Yilgarn Block from the uplifted, marginal plateau" (Gordon & Lewis 1980). In the physiographic context of the present paper, the seismic zone would be expected to lie between the Median Watershed and the Darling Range uplift zone, but a contrasted overlay of the boundaries (Fig 6) shows that this is not entirely the case. While the Median Watershed shows some parallelism with the eastern boundary of the seismic zone, the western uplift continues much further north and transgresses the seismic zone.

The profile of the Yilgarn River (Fig 3) shows that the grade does not steepen west of the Caroline Gap as would be expected if there had been down-warping. While Fig 3 shows the present surface, Salama's (1997) data equally show no steepening of the palaeochannel. However a possible explanation which would account for the Pliocene dates of his samples may be that when the drainage from the interior broke through the Caroline Gap the site of the Yenyening Lakes stood higher and the



Inselbergs in the Darling Range, with heights in metres

Shoulder of Mt Saddleback	593	White Horse Hills	500, 480
Mt Saddleback	577	Eagle Hill	481
Mt Solus	574	Mt Keats	474
Mt Cooke	571	Drivers Hill	461
Mt Wells	547	JDI	438
Mt Dale	546	CK5	434
Boonering Hill	529	Spion Kop	427
Mt Randall	525	Mt Curtis	413
Mt Cuthbert	509	George Hill	401
Mt Vincent	≈ 500		

Figure 7. Location of Monadnocks > 400 m in the Darling Range.

river was able to flow directly through into the upper Avon. If later there was a local down-warp affecting the Yenyening Lakes area, the renewed pluvial conditions of the Pliocene, shown *inter alia* by local deposits at Lake Tay (Bint 1981) and nearby Lake Toolibin (Milne 1998), could have caused the accumulation of the substantial valley fill recorded by Salama (1997). It was probably at this stage that Salama's "huge lake" was in existence to absorb the Pliocene sediments which are not in evidence downstream on the coastal plain. The Middle Eocene is the most recent interval during which significant drainage can be demonstrated in the Perth Basin (Quilty 1978).

Reverting to Fig 5, the present situation (Stage 4) is not greatly different from Stage 3. The Yenyening Lakes have filled with sediments surfaced with a chain of playas. The Darkin Swamp has also partly filled with sediment. The plateau level on the Darling Range is thickly duricrusted and seems not to have been modified since Eocene time. Although the fossil evidence of Hill & Merrifield (1993) demonstrates the presence of rain forest with *Nothofagus* and several species of conifers in the Eocene, thereafter rainfall in general together with stream activity appear to have declined materially in an episodic fashion, generally dry in the Miocene, humid in the Pliocene.

King (1962) noted that monadnocks on the Darling Range exceed the height of those further east in the wheatbelt country. A number of impressive inselbergs (mainly granite) of outstanding height are restricted to an area on the Pinjarra map sheet between Lat 32° and 33° and between Long 116° 00' and 116° 30', within 50 km of the Darling Fault (Fig 7). The watersheds range between 300 and 400 m in height except where inselbergs are included and indicate a general plateau level of about 400 m; 21 points exceed this height, 11 of them exceeding 500 m, with a maximum of 593 m on part of Mt Saddleback. Perhaps not all of these are strictly inselbergs with exposures of bare rock, as some will be forested hills capped with duricrust. Mt Wells and Mt Saddleback consist of basalt, not granite. The only other high points in the Darling Range are Russel Top (422 m) and Morangup Hill (477 m), situated north and south of the Avon below Toodyay. All are certainly higher than inselbergs further east such as Mt Caroline (340 m) and Mt Stirling (365 m), and even massive outcrops like Billyacatting Hill (400 m) near Kununopping which covers several square kilometres. They may therefore be held to demonstrate uplift, of up to 200 m, but it must be clear that they already protruded from the general level before uplift took place, and that their exposure is not due to denudation since uplift. The higher ground in the Darling Range is thickly mantled with ferruginous duricrust, and denudation since uplift is held to have been moderate. Concentration of inselbergs in this part of the Range is most likely due to their occurrence in the Pinjarra Orogen (Myers 1990b).

The palaeodrainages as developed during the Eocene, that is to say after retreat of the Cretaceous high sea level and before the Late Eocene uplift, are shown in Fig 8. The uppermost tributaries of the Mortlock River North Branch flowed west to the Moore River. Those of the South Branch continued south-west from present Lake Walyourmouring to join the North Branch. The Brockman River created the Chittering valley by exploitation of the Chittering Metamorphic Belt. The Mortlock River Branches and the proto-Avon similarly exploited the Jimperding Metamorphic Belt. Their valleys were widened and deepened. The ancestral Yilgarn River continued west from the Yenyening Lakes area, uniting with the upper Avon and Dale Rivers, across the present Darling Range. Further south the Arthur and Beaufort Rivers flowed into the Collie catchment. Disappearance of the Dandaragan plateau in the southern Perth Basin led to down-cutting by the lower courses of all these rivers.

After the uplift the rivers adjusted their courses to those of the present day (Fig 1). The headwaters of the Moore Rivers were diverted to the south as were those of the Mortlock North Branch. In its lower course the latter was moved further to the east, joining with a formerly separate Middle Branch (Fig 8). The Avon and Dale Rivers abandoned their course across the Darling Range and developed a new route to the Mortlock which already had its own outlet across the Darling Range. The Murray River seems to show the least evidence of disruption by uplift, probably because the catchment does not extend so far east as the others and was uplifted

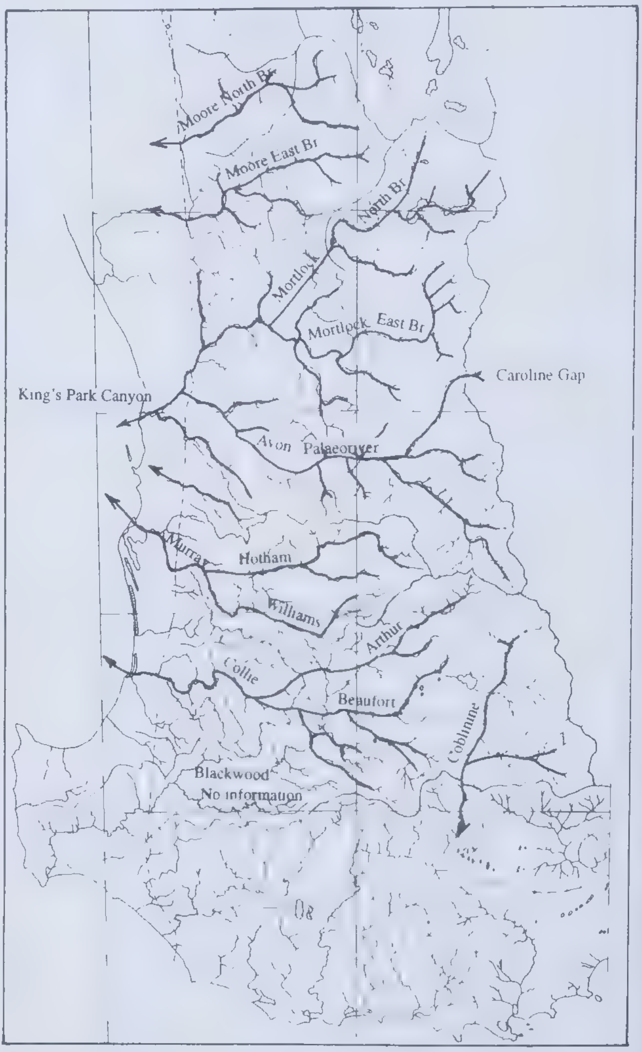


Figure 8. Palaeodrainage of the West Coast Systems, epoch Palaeocene (bold lines). The submarine Perth Canyon is located west of this diagram.

as a whole. There is some indication (Fig 8) of diversion of the Hotham River. The palaeochannels of the Arthur and Beaufort Rivers, having filled with sediment, developed a new outlet through the Blackwood.

Conclusions

1. Drainage of the central Yilgarn System is confined by two north-south watersheds, the Central Watershed of Beard (1998) and the Median Watershed defined here. These constitute a bifurcation of the central watershed of the Western Shield. Drainage of this area which today is mostly intermittent or inactive, is gathered from the north, east and south to escape to the west through a single point, the Caroline Gap, in the Median Watershed and joins the Avon River. The shape of the Yilgarn catchment, prevalence of north-south alignments, and in the south conspicuous alignments with rivers draining to the south coast suggest that drainage of the System originally flowed in a southward direction. The Yilgarn System is bounded on the south by a watershed parallel to the south coast, formerly named the Jarrahwood Axis. This name is now found inappropriate.
2. The South Coast Watershed formed in the middle to late Cretaceous by marginal uplift of the craton during separation from Antarctica causing reversal of former southerly drainage. This reversal appears to have been assisted by a contemporary downwarp across the northern part of the Yilgarn System along a line termed the Chin-Smith Lineament. Prior to the south coast uplift the south-flowing rivers incised canyons into the rifted margin of the continental platform.
3. Subsequent to uplift forming the South Coast Watershed the continental margin sagged towards the rift forming a slope (the Ravensthorpe Ramp) which continues to the edge of the continental shelf and has carried down the canyons to become the submarine canyons of today. This situation is most clearly defined south of the Yilgarn System. Further west there is a secondary axis of uplift, the Stirling Range Axis, about 50 km south of the south coast watershed. Further east there is evidence for an additional south-flowing former palaeoriver, the Woolgangie, which has been truncated by capture by the Lefroy-Cowan system.
4. Drainages to the west coast formed in the Mesozoic bounded inland by the Median Watershed and contributing sediment to the Perth Basin. In the Early Cretaceous there was an uplift associated with continental separation on the west. An extensive canyon (the Perth Canyon) was incised at the edge of the rift and later drowned. High sea level prevailed in the Perth Basin until the late Cretaceous when regression promoted rejuvenation of the rivers. A deep valley was cut by the lower Avon River into sediments of the Perth Basin but was drowned and filled after subsidence of the Swan Syncline. The Brockman River, Mortlock River North Branch and the Avon from Beverley to Toodyay owe their alignments to exploitation of the Chittering and Jimperding Metamorphic Belts.
5. In the Late Eocene a marginal uplift of the craton by 150-200 m took place in a belt 80 km wide east of the Darling Fault creating the Darling Range and causing diversions of drainage. Headwaters of the two Moore Rivers (north and east branches) were cut off and diverted to the south. Headwaters of the Mortlock River (north branch) were similarly diverted and the lower course of the Mortlock was relocated some distance to the east. The combined Avon and Yilgarn Rivers which formerly flowed due west were diverted north to join the Mortlock in a new course through the Darling Range. Similarly the Arthur and Beaufort Rivers were diverted from the Collie System and found a new outlet through the Blackwood River. Depth of the palaeochannel beneath the Avon-Yilgarn affords proof of the uplift of the Darling Range as there would otherwise have been no outlet. It is probable that there was a later local down-warp associated with the South West Seismic Zone in the area of the Yenyening Lakes which then accumulated substantial thickness of sediment during a Pliocene pluvial interval. Monadnocks in the Darling Range which can also be cited as evidence for uplift have been identified and mapped.

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Clay soil fulgurites in the Eastern Goldfields of Western Australia

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Abstract

Discovery of two fresh lightning strikes in the Eastern Goldfields of Western Australia and observation of their features is considered to have confirmed that samples of highly vesicular glass regularly observed in this area of Western Australia are fulgurites. It is proposed to refer to them as "clay soil fulgurites" to distinguish them from the "sand fulgurites" which have been more readily identified and collected. One of the strikes was notable for the disturbance caused to the soil. Observations of this feature of the strike suggested that the moisture content of clay soils and subsoils plays an important role in determining the path taken by the electrical discharge and the production of fulgurites. This factor is considered to modify the primary features such as the intensity of a particular lightning discharge and the composition of the soil. The second strike resulted in a large vesicular glass fulgurite that is described here and has been presented to the Western Australian Museum.

Introduction

Lumps of glassy vesicular material lying on the surface of the ground are commonly found by geologists during fieldwork in the southern parts of Western Australia. Many of these glassy fragments appear to have been lying exposed for some time and have an abraded appearance with surfaces covered in the red dust typical of the soils of the region. The size of these fragments varies; most are hand-sized but a few are somewhat larger. When visible the glass is usually a streaky grey to dull green to brown colour. These fragments are highly vesicular and light in weight. Trendall (1964) described a number of samples of similar glass in the collection of the Geological Survey of Western Australia and presented details of their microscopic structure and chemical composition. On the basis of a thorough review of the available data, Trendall (1964) concluded that they were probably formed by the fusion of soil by lightning, and suggested the name "fulgurite slag" for the material. I have noted these objects during work in central Africa and considered that were probably fulgurites, but had never observed them in a situation that provided any direct evidence of their origin.

This paper describes two specimens of glassy material, which apparently were discovered shortly after formation as indicated by observations of their occurrence. Their features are consistent with the fusion of clayey soil by lightning, and the name "clay soil fulgurite" is therefore suggested to distinguish them from other varieties such as the better-known "sand fulgurites" (*e.g.* Glover 1974).

Observations

First Discovery

In June 1984, the author was mapping on Avoca Downs Station, north of Randall on the Trans Australia Railway Line. There had been thunderstorms in the area and what was interpreted to be a very recent lightning strike was recognised. The lightning had struck the ground on a low rise in a clearing amongst gum trees with only a very low and sparse vegetation covering the ground. The soil profile in the vicinity of the strike was complete with a surface crust of lichen and vegetation that has been destroyed on most pastoral areas. The point at which the deduced lightning discharge appeared to have entered the ground was marked by a small area less than 50 cm across where the ground surface had been greatly disturbed with small clods of soil having been thrown out onto the surrounding surface. On the patch of disturbed soil a fulgurite of partially fused material with a vesicular structure was lying. This was also judged to have been thrown into the air and to have dropped back onto the disturbed soil. The salient features of this strike are illustrated in Fig 1.

While there was some fused glassy vesicular material present in the core of this fulgurite, the outer portions were composed of baked or dried clay which also had a vesicular structure and which was very fragile and crumbled in the hand. Of equal, or even greater, interest was the observation that the small patch of disturbed ground formed the top of a very low conical mound with cracks in the soil radiating out from it (Fig 1). The diameter of the cone was about six metres and most of the ground surface was essentially intact with some small cracks and a slight unevenness of the surface. On walking on this area the surface gave way underfoot with my boot sinking up to 50 mm near the centre of the cone. It was the lack of any significant ground cover that allowed this feature to be recognised.

From the observations made of the features of the occurrence on Avoca Downs it is considered that the origin of these vesicular glass objects is most likely to be from lightning strikes and that they are therefore a variety of fulgurite. The Avoca Downs example only produced a small crumbly fulgurite but this discovery

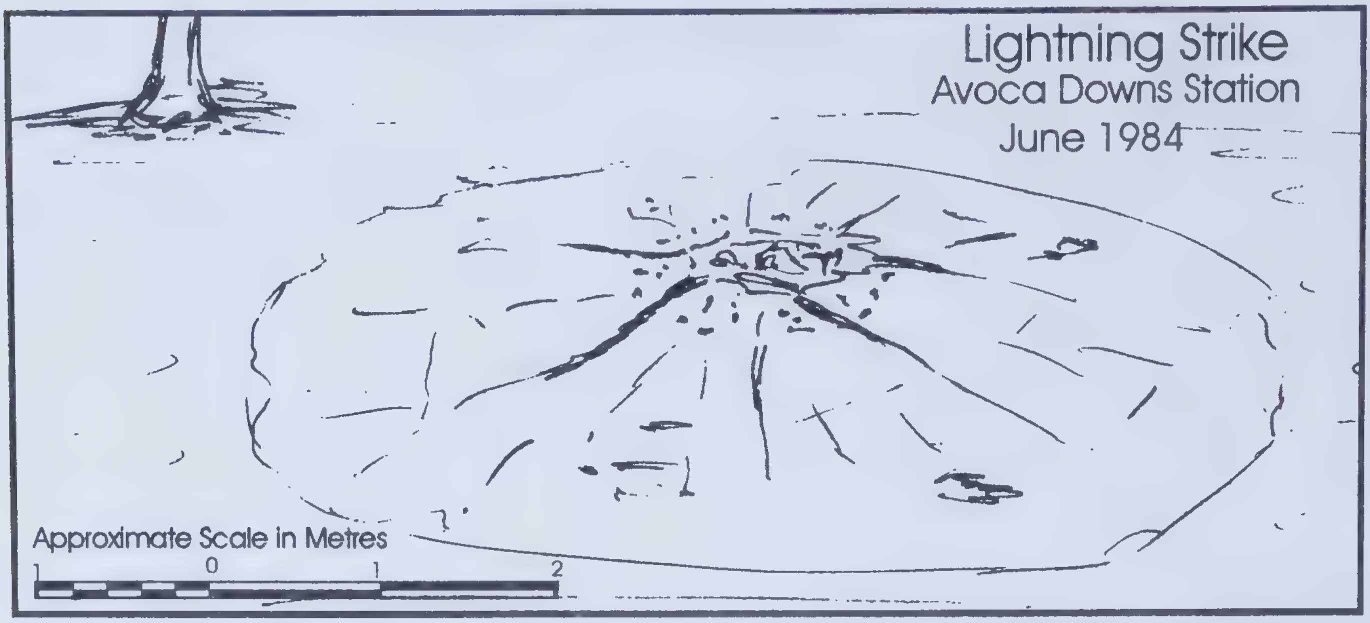

Figure 1. Sketch of the structure that resulted from the Avoca Downs lightning strike. The sub-surface soil has been expanded to a maximum of about 50 mm at the centre of the cone where the soil has been significantly disturbed with lumps having been thrown into the air.

renewed my interest in these objects. Study of further such objects found lying on the surface in this region of the goldfields revealed that a significant proportion of them exhibit a zonal structure, with a core of fused glass that grades outwards into less fused and more crumbly material. The remaining specimens appeared to be more highly fused but of course this might not be an original feature and these might be the cores of a larger fulgurites that had suffered erosion. Although this could be the case for some samples, a large proportion were judged to have an original glassy exterior extending over varying proportions of their surfaces. It is therefore possible to distinguish two morphologies of these fulgurites, one which has a glassy core grading outwards into baked clay and the other which is virtually totally composed of glass and has a glass skin extending over a variable proportion of its surface.

Second Discovery

In May 1986 the author was mapping in the Eastern Goldfields near Mulgabbie Hill on Pinjin Station about 190 km north east of Kalgoorlie and approximately 60 km north of the Avoca Downs strike described above. Here, shortly after some thunder storms, a large recently formed mass of vesicular glass was found on the surface of the ground surrounded by the remains of an old tree stump. The inside surface, of what had once been part of a hollow trunk, was covered in charcoal and all that remained was a thin shell of wood with a jagged profile rising to a point about 2 m above the ground. The object was lying on the surface of the ground within this shell and was formed of jet black glass that had been formed recently since there was no sign of any dust on its surface. It was only in contact with the ground in two main areas and the concavities in the lower surface formed spaces between the vesicular glassy material and the surface of the soil. When found it had some teardrop shaped pieces of glass hanging by thin glass threads from the under side. The observed features of the object and its setting led to the conclusion that it is a fulgurite. The underlying ground was loose soil containing charcoal fragments. It would appear from its position when found that, like the Avoca Downs fulgurite, it too had been thrown into the air at the moment of formation. Unlike the Avoca Downs occurrence, the Mulgabbie strike had not resulted in any visible widespread disturbance of the ground surrounding the strike outside of the old stump. The soil was loose and uncompacted inside the stump, which was probably a result of the lightning, but it is not known what condition it was in before the strike.

The Mulgabbie fulgurite is of fairly uniform thickness (generally less than 100 mm thick) but bent and irregular in shape; its maximum dimensions are just over 400 mm long by 300 mm across (Fig 2). When collected in 1986 the glass was black with a high vitreous lustre and very spectacular. A tear drop of glass that detached from the underside of the fulgurite still posses the black, vitreous lustre (Fig 2B)

The specimen is composed almost entirely of glass. Minor areas of the surface have reddish soil sticking to them with one of the largest soil patches on one end suggesting that this may have been the main area of contact with the ground immediately after the strike. A significant proportion of the surface area of the fulgurite may be described as mammillated to botryoidal with the glass forming an almost continuous surface. Other areas have a "damaged" appearance with the internal vesicular structure visible. These surface types are shown in Fig 2C.

Since collection, the glass has started to devitrify and is now a dull, dark grey with a streaky appearance. Some areas of glass have the greenish-brown colours that the author has noted in some of the older fulgurites that he has observed. The Mulgabbie specimen weighs just under 3 kg. It has been donated to the Western Australian Museum.

Factors modifying the effect of a lightning discharge

There are a number of factors that could determine the characteristics of a fulgurite formed by a particular strike.

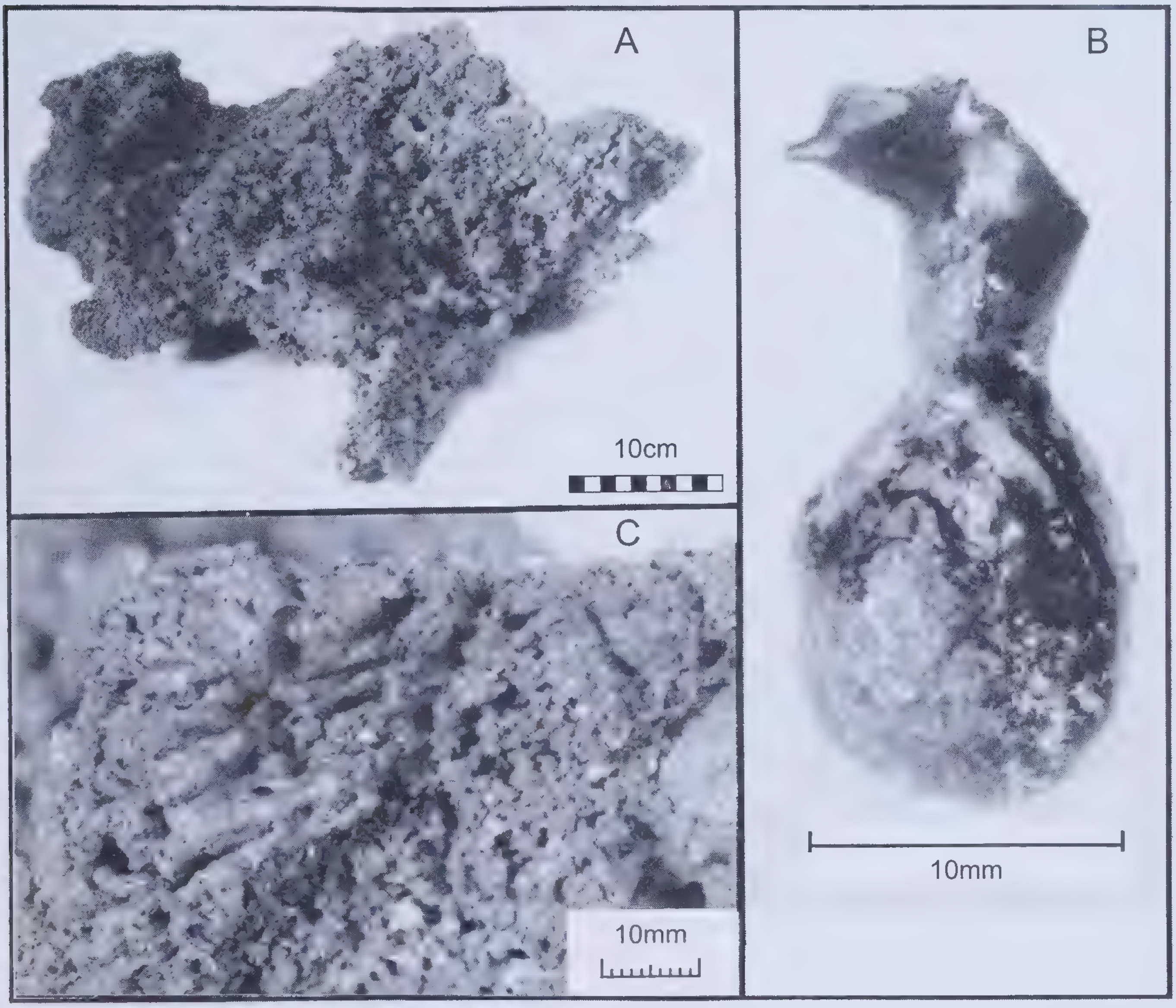

Figure 2. A: General view of the Mulgabbie fulgurite showing lower surface as found (scale bar = 10 cm). B: Glass tear drop which was hanging from lower surface by a glass thread when found (scale bar = 10 mm). C: Surface detail showing smooth sealed areas and areas with open vesicles (scale bar = 10 mm).

The primary factors are the energy of the discharge and the composition of the soil at the locality. Another significant factor is the conductivity of the soil. Sands are usually damp below the surface layers and I suggest that the reason sand fulgurites have their vertical narrow tapering form is that the sand is normally uniformly conductive so the discharge takes the shortest path and travels straight down. Lightning strikes in sand form narrow inverted conical tubes of silica glass that have been commonly traced to depths of over one and a half metres with a tapering diameter from 20 mm at the top to 3 mm at the bottom (Beasley 1963). In exceptional circumstances they have been traced up to 20 m deep (Bouska 1993). As the electrical discharge flows down into the damp sand the current is able to disperse, sometimes producing root-like protuberances of glass, and steadily becomes less intense with depth.

In the case of the Avoca Downs occurrence, the observed features are considered to support the interpretation that at the time of this strike there had been rain after an extended period of dry weather. The ground at depth was therefore dry with a shallow damp surface layer due to recent rain. This would allow the electrical discharge to radiate out within the shallow and more conductive damp surface layer of soil. The discharge caused considerable heating that resulted in the development of steam and heated gases within the soil that expanded and raised the low conical structure. The radial dispersion of the electrical current may also have resulted in a less confined current at the point of entry of the discharge into the soil and consequently the reduced development of glass, and zoned structure, in the fulgurite that was formed.

Comparison of the two strikes

Comparing the Avoca Downs strike with that at Mulgabbie I considered that the latter was probably a more intense electrical discharge. It produced a large vesicular glassy fulgurite that was thrown into the air by escaping steam and hot gases. It had cooled sufficiently by the time that it sank back onto the surface of the ground to maintain much of its shape with only minor areas in contact with the soil. The presence of the charcoal-covered wood sticking up out of the ground was probably a major factor in attracting the lightning discharge to this spot but there is no evidence to suggest the stump had burned to any significant extent at the time of the most recent strike.

The Avoca Downs strike may have been less intense and/or the energy of the discharge was dispersed due to the electrical current spreading out radially from the point of impact. The fulgurite formed was small and consisted of a glassy vesicular core surrounded by baked clay, which also had a vesicular structure. The observations made of the considerable disturbance to the surface layers of the soil surrounding this strike are considered to suggest that the distribution of moisture in clay soils can control the path taken by a lightening discharge and may be an important factor in determining the results of a particular strike.

Conclusions

The observations that were made at the sites of these unusual occurrences, and of the glassy objects produced, are considered to indicate that they resulted from lightning strikes. They are considered to have confirmed that the fragments of glassy vesicular material that are found in the Eastern Goldfields are fulgurites from old lightning strikes. These vesicular fulgurites, which are formed when lightning strikes a clay soil, are very different from the narrow tapering silica tubes produced by lightning striking sand. They have not received the same attention as the sand fulgurites because once this type of fulgurite has been exposed to weathering for some time its origin is not obvious. As they are typically found lying loose on the surface, it is also not possible to determine if they are *in situ* or have been transported from elsewhere. The dark glass that forms the clay soil fulgurites and their vesicular character results from the different chemical composition of the clay soil compared to the relatively pure silica composition of many dune sands. It is suggested that these fulgurites be referred to as "clay soil fulgurites" to distinguish them from the "sand fulgurites". A search of the references to fulgurites reveals that the majority of these papers refer to fulgurites that were formed by lightning strikes either in sand or in rock exposed on the peaks of hills and mountains, and the only reference that I have been able to trace describing "clay soil fulgurites" is that by Trendall (1964).

My observations on the Avoca Downs and Mulgabbie Hill occurrences of vesicular glass, and the associated phenomena, are considered to indicate that they resulted from recent lightening strikes. Although neither site was "still steaming" (which is the ultimate grade of freshness when it comes to lightning strikes) they were perfectly preserved and were judged to be days old rather than weeks old. These observations raise a number of questions about the behaviour of lightning discharges in dry clay soils with damp layers. It is hoped that further observation and interpretation of the results of fresh lightning strikes, by scientists who discover them while working in the field, will be able to confirm and increase knowledge of their behaviour in clay soils in various conditions.

Acknowledgements: The author wishes to acknowledge the expertise of K Brimmel of the Western Australian Museum for the fine photographs of a very difficult subject.

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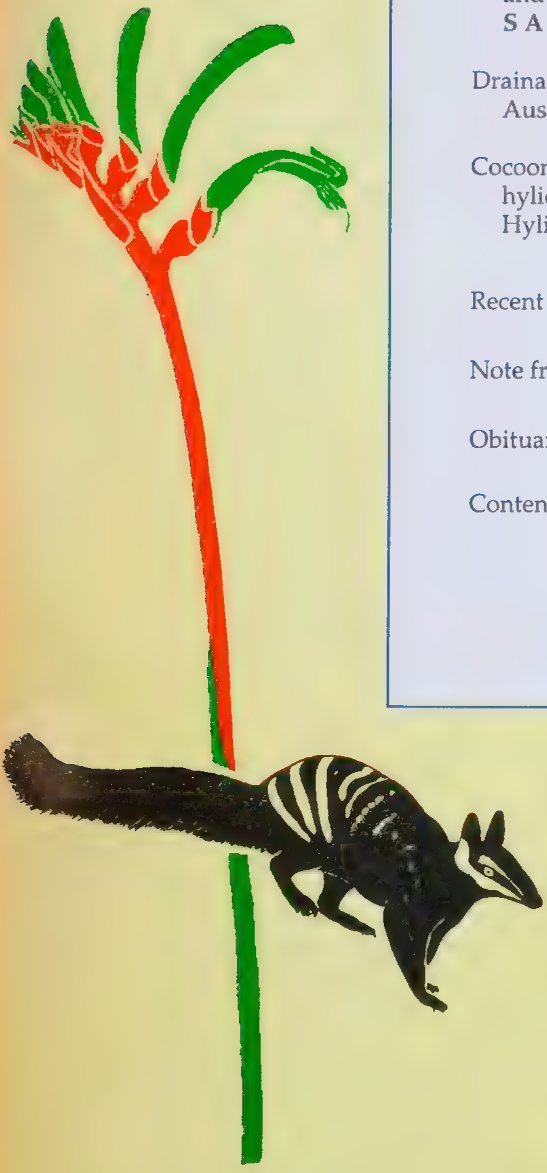

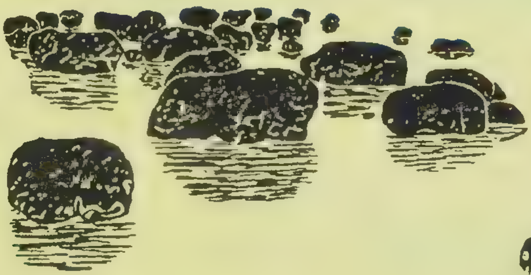

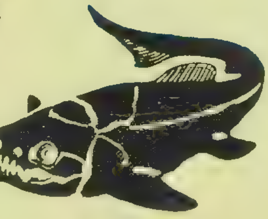

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor) and the Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

Journal of the Royal Society of Western Australia, 83:1-11, 2000

Threatened plant communities of Western Australia. 1. The ironstone communities of the Swan and Scott Coastal Plains

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Abstract

The restricted plant communities of the massive ironstones (ferricretes) of the Swan and Scott Coastal Plains are described. These communities are amongst the most threatened in Western Australia. Much of the original extent of these communities has been cleared for agriculture, the remaining areas are threatened by *Phytophthora cinnamomi*, grazing and activities associated with mineral exploration. Twenty taxa have been recorded as being endemic to or having their major distribution centred on these ironstone areas, a further three taxa may have forms restricted to this habitat. Only eight of these 20 taxa are known from secure conservation reserves. Major differences in community composition were related to geographic and edaphic factors. Species richness ranges from an average of 14 to 67.8 taxa per 100 m^2 across the nine community types described. Only five of these community types have been recorded from secure conservation reserves. Most occurrences of these plant communities occur on ironstone areas which are much younger than the Tertiary aged laterites of the nearby Darling and Blackwood Plateaus.

Keywords: threatened community, ironstone, ferricrete, endemism

Introduction

While much has been written on the massive land clearance and loss of biodiversity of the Western Australian wheatbelt (Main 1987; Saunders & Curry 1990; Hobbs & Saunders 1994) until recently little attention has been paid to similarly impacted plant communities of the Swan Coastal Plain and the Scott Coastal Plain (Gibson *et al.* 1994; Smith & Ladd 1994; Robinson & Keighery 1997). Recent work has shown that over 95% of the fertile soils of the Swan Coastal Plain have been cleared for agriculture, a figure on par with the clearance level in the wheatbelt (personal communication, AH Burbidge & J Rolfe, CALM). Of particular interest are the recently identified ironstone communities on the Swan Coastal Plain and Scott Coastal Plain that have been massively impacted by land clearance and are generally characterised by restricted endemic taxa (Anon 1990; Gibson *et al.* 1994; Smith & Ladd 1994; Robinson & Keighery 1997). These communities are winter wet shrublands that occur on skeletal soils over the massive ironstone on the coastal plains and the foot slopes of the Whicher Range. While the existence of this geomorphological unit has long been recognised (de la Hunty 1960; Baxter 1977; Tillie & Lantzke 1990; McArthur 1991) the conservation significance of the associated plant communities has not been assessed.

The term laterite has been applied to this geomorphological unit (Johnstone *et al.* 1973; Mulcahy 1973) but is avoided here because this unit do not posses the classic pallid zone clay layer over bedrock (seen typically on the nearby Darling and Blackwood Plateaus) and are believed to be currently forming (Johnstone *et al.* 1973), contrasting with the Tertiary age of most of the laterite of the adjacent Plateaus. In this paper the term ironstone is used to describe the massive ferruginous landform unit on the Swan and Scott Coastal Plains and foot slopes of the Whicher Scarp (Tille & Lantzke 1990) and the term laterite describes the common landform on the old deeply weathered uplands of the Darling and Blackwood Plateaus. The ironstones are believed to have been formed by the precipitation of iron from the ground water mainly in the zone of water table fluctuation (Baddock 1995; Tille & Lantzke 1990; Anand 1998). They may be several metres thick overlying deep sand profiles (Belford 1987; Baddock 1995). Descriptions of soil profiles on these ironstones are given by de la Hunty (1960), Tille & Lantzke (1990) and McArthur (1991). Anand (1998) has described a similar unit on the upper valley slopes of the Darling Plateau as vesicular ferricrete, which is quite different in chemical composition from the older adjacent lateritic residuum. The aim of the present paper is to describe the flora and vegetation of the coastal plain ironstones and to determine their conservation status.

Methods

Study Sites

The southern half of the Swan Coastal Plain is a narrow belt of primarily Quaternary sands stretching 400 km from the Moore River to south of Busselton. This plain is interrupted by flood plains of a number of river systems draining off the Darling Plateau. It is these fertile

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plains that have been preferentially cleared for agriculture. The coastal plain is bounded by the Indian Ocean to the west and the Darling and Whicher Scarps to the east and south. Iron rich impeding layers are common at depth on most soil types on the coastal plain resulting in variety of sumplands and damplands. However, vegetation typical of skeletal soils over massive surficial ironstone is much more restricted.

These ironstones are generally found along the base of these scarps although they can extend some distance out onto the coastal plain. They are much more restricted than depicted by Mulcahy (1973) who includes the alluvial soils of the eastern side of the plain in his low level laterite unit. The only extant areas of vegetation on ironstone on the southern coastal plain are a small area (*ca* 10 ha) near Gingin some 80 km north of Perth (original extent was *ca* 20 ha, estimated from aerial photographs), and *ca* 68 ha on the southern end of the plain south of Busselton (originally *ca* 2130 ha, mapped by Tille & Lantzke 1990).

The Scott Coastal Plain, extending from Augusta east to Walpole, is a very similar land system to the Swan Coastal Plain. The ironstone areas of the Scott Coastal Plain are apparently restricted to the western end of the plain near Scott River occurring as far east as Black Point. About 360 ha of the original 1780 ha remain uncleared.

The current extent of ironstone communities was determined by the intersection of remnant vegetation on recent aerial photography with land unit mapping of Tille & Lantzke (1990) (with some minor correction). Twenty eight 10 m x10 m plots were established in the three ironstone areas (Fig 1), one on Gingin ironstones, 11 on the Busselton ironstones and 16 on the Scott ironstones. All vascular plants were recorded within each plot. While most sites were visited on at least two occasions, some sites were visited only once in late spring when herbs and grasses were easily identifiable. In addition to flora lists, information was collected on vegetation structure, slope, aspect, degree of waterlogging and vegetation condition. Sites and species (occurring at two or more sites) were classified using Bray-Curtis association measure and UPGMA fusion algorithm to define community types and species groups (Sneath & Sokal 1973). Only taxa identified to specific level were included in the analysis.

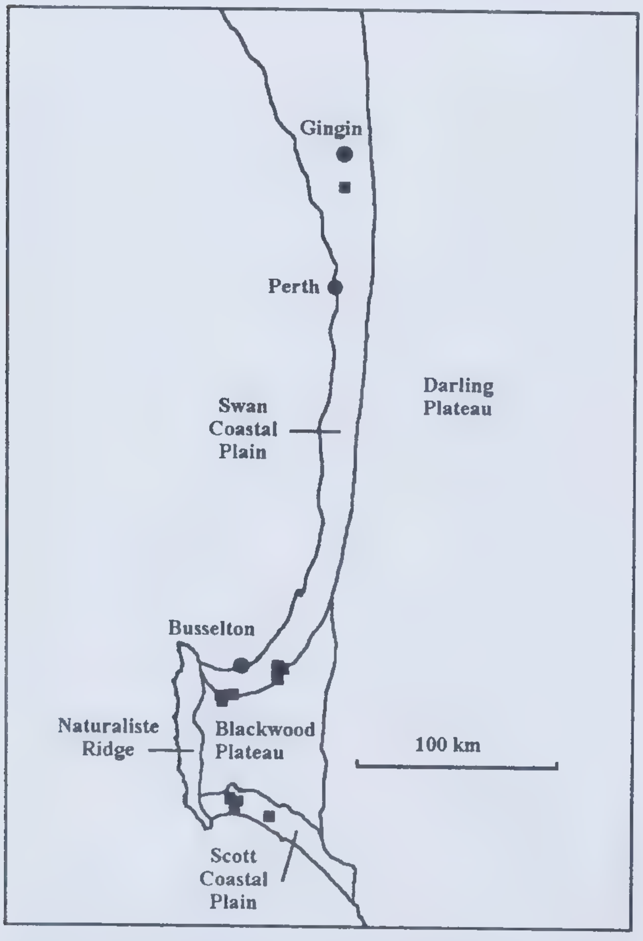

Figure 1. Map showing location of the 28 plots on massive ironstones and boundaries for the major geomorphological units. (Solid square may indicate more than one quadrat).

In addition to these 28 floristic sites, all extant ironstone patches on public lands on the Swan and Scott Coastal Plains were visited and species were noted. Complete surveys of most ironstone areas on private property have not yet been undertaken. From these data and with reference to collections held in the Western Australian Herbarium, a list of endemic taxa and taxa whose distribution is centred on the ironstone taxa was compiled. Nomenclature generally follows Green (1985) and current usage at the Western Australian Herbarium. Voucher specimens have been lodged in the Western Australian Herbarium.

Results

Flora

A total flora of some 400 taxa has been recorded from the 28 plots in the three ironstone areas, 48% of which were only recorded at a single site. Of the 400 taxa, 20 are either ironstone endemics or have their distribution centred on the ironstone areas. Eleven of these taxa are restricted to the Busselton ironstones, five occur only on the Scott ironstones and four taxa are shared between these areas (Table 1). A further three taxa *Opercularia* aff *vaginata* (BJK & NG 238), *Calothamnus* aff *quadrifidus* (BJK & NG 230), *Lepyrodia* aff *macra* (BJK & NG 1026)) also appear to be restricted to the ironstones but require further taxonomic study to fully clarify their relationships. There do not appear to be any endemic taxa on the Gingin ironstones.

Many of the ironstone endemics are recently recognised taxa and most are currently listed on the schedule of Western Australian's most threatened flora (Government Gazette, 14th July 1998). *Grevillea mccutcheonii* is, for example, restricted to a single population on a weedy road reserve and is known from only three adult plants, while *Lambertia echinata* subsp *occidentalis* is known from a single population of seven adult plants is an area badly infected by the root rot fungus *Phytophthora cinnamomi*.

Six of the 20 taxa confined to or centred on the ironstones (*Brachysema papilio*, *Darwinia* sp (GJK 12839), *Grevillea mccutcheonii*, *Lambertia echinata* subsp *occidentalis*, *Darwinia ferricola* ms, and *Melaleuca* aff *incana* (NG & ML 593) are known from only one population and these populations number from three adult plants to several thousand. *Lambertia echinata* subsp *occidentalis* occurred

Table 1

Taxa restricted or largely restricted to ironstone areas, their distribution and conservation status (Government Gazette,14th July 1998). + indicates presence, E indicates endemic on ironstone, R indicates declared rare flora.

Taxon	Swan Coastal Plain	Scott Coastal Plain
Andersonia ferricola ms	$+^{E}$	
Brachysema modesta	$+^{R}$	
Brachysema papilio	$+^{ER}$	
Chamelaucium roycei ms	$+^{R}$	
Darwinia sp (GJK 12839)	$+^{ER}$	
Dryandra squarrosa subsp *argillacea*	$+^{ER}$	
Grevillea elongata	$+^{ER}$	
Grevillea mccutcheonii	$+^{ER}$	
Hakea sp (BJK & NG 226)	+	
Lambertia echinata subsp *occidentalis*	$+^{ER}$	
Petrophile latericola ms	$+^{ER}$	
Dryandra nivea subsp *uliginosa*	$+^{ER}$	+
Calothamnus aff *crassus* (Royce 84)	$+^{E}$	+
Chordifex isomorphus	+	+
Loxocarya magna	+	+
Darwinia ferricola ms		$+^{ER}$
Grevillea aff *manglesioides* (GJK 15158)		$+^{E}$
Hakea tuberculata		+
Lambertia orbifolia		$+^{R}$
Melaleuca aff *incana* (NG & ML 593)		$+^{E}$

on somewhat deeper soils than was typical for the ironstone endemics.

Lambertia orbifolia and *Hakea tuberculata* are both known from several populations on the Scott Plain and have disjunct outlying populations in the Albany area some 250 km to the east. The Albany populations of *Hakea tuberculata* occupy a variety of habitats including winter wet flats on both ironstone and sandy substrates, while the *Lambertia orbifolia* population occurs on Tertiary laterite. *Chordifex isomorphous* has been recorded on the ironstones of both the Swan and Scott Coastal Plains as well as further disjunct populations between Mt Barker and Ravensthorpe (250 - 450 km to east) on sand and laterite substrates (Meney & Pate 1999).

Vegetation

Classification of the twenty eight floristic plots shows nine recognisable groups, here called community types (Fig 2). These community types are strongly correlated with geography and edaphic factors and to a lesser degree vegetation condition. The dendrogram shows the nine community types divide into three groups. Community types 1 to 4 occur on shallow sands and loamy sands on massive ironstones. Community types 1 to 3 occur at the base of the Whicher Scarp on the Swan Coastal Plain, while community type 4 occurs on the Scott Plain. The second group consists of community types 5 and 6 which occur on sands over massive ironstone on the Scott Plain and community type 7 which is the floristically distinct northern ironstone site. The final group is the species poor community types 8 and 9 which are restricted to the Scott Plain (Table 2).

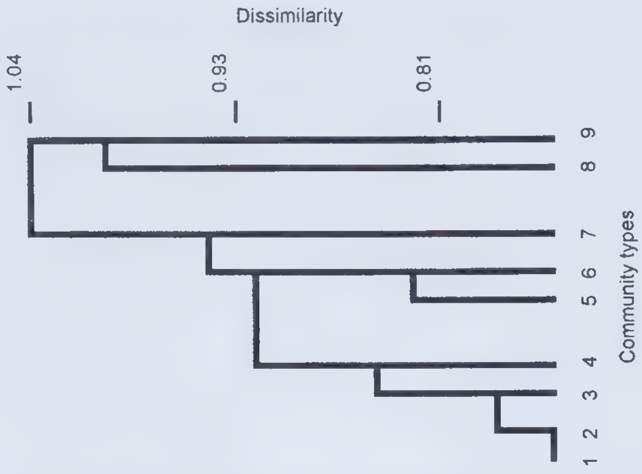

Figure 2. Dendrogram of the nine community types occurring on ironstone on Swan and Scott Coastal Plains.

Table 2

Mean species richness per plot (calculated on full species lists) and number of plots classified into each of the nine ironstone community types found on the Swan and Scott Coastal Plain ironstones.

Community type	Species richness	Number of plots
1	67.9	4
2	48.0	3
3	38.5	4
4	50.7	7
5	44.0	1
6	27.0	1
7	42.0	1
8	27.3	6
9	14.0	1

- **Community type 1** occurs on the massive ironstones to the south of Busselton on skeletal soils. This soil layer is generally less than 1 cm deep and is often absent. This community type was the most diverse, with a mean species richness of 67.9 species per plot and was characterised by species groups B and N (Appendix 1) which are particularly rich in herb species. Herbs such as *Angianthus preissii, Aphelia nutans, Siloxerus filifolius,* and *Stylidium emarginatum* appear to be restricted to this community type.
- **Community type 2** is found on the ironstones south of Busselton on slightly deeper and sandier soils. At these sites the herb layer is not as rich (e.g. lower representation of species in species groups B and N) and species such as *Lyginia barbata, Regelia ciliata* and *Chordifex serialis ms* and other species in species group L are more common.
- **Community type 3** occurs on deeper (to 10 cm) loamy sand soils on the ironstones south of Busselton. The shrub layer tends to be denser and many of the herbs seen in the two previous groups do not occur here (Appendix 1). Species groups C and G characterise this group as does the complete lack of species in species group N. Mean species richness is lower than the previous community types (Table 2).
- **Community type 4** consist of the species-rich massive ironstones of the Scott Plain. This community type shares species group B with the three Busselton groups but is differentiated by occurrence of such

species such as *Calothamnus* aff *crassus* (Royce 84), and *Velleia trinervis* in species group H, by a higher representation of species in species groups A, D, E as well as low frequency occurrence of species in species group C, K and N. This community has a higher species richness (average 50.7 species per plot) than any other community except the massive ironstones below the Whicher Scarp (type 1).

- **Community types 5 and 6** occur on the Scott Plain on more sandy substrates over massive ironstone; both are represented by only single plots. Community type 5 is species rich (Table 2) and is characterised by low representation of species in species group B and high representation of species in species group J (Appendix 1). Of the 44 taxa recorded at this site, 21 were restricted to it. Community type 6 in contrast is relatively species poor and is characterised by species group F. This site occurred close to the coast which is reflected by the presence of taxa such as *Agonis flexuosa*.
- **Community type 7** was also represented by a single site on the small area of ironstone north of Perth near Gingin. This community is characterised by a rich herb layer with carpets of Asteraceae (*Rhodanthe manglesii, Rhodanthe spicata* and *Myriocephalus helichrysoides*) a general lack of shrub layer. Of the 42 species recorded at this site 22 were not recorded from other ironstone areas.
- **Community type 8** occurs on massive ironstones on the Scott Coastal Plain. This community type is typically a dense tall shrubland with low species richness (Table 2). The closed nature of this community precludes the rich and diverse herb flora (especially in species group B) evident in the more open community type 4 which occurs on similar massive ironstones elsewhere on the Scott Plain. Taxa in species group H were most typical of this community type and contained the only sites where the ironstone endemic *Grevillea* aff *manglesioides* (GJK 15158) and *Boronia anceps* were recorded.
- **Community type 9** is represented by a single plot in a deep winter wet swamp dominated by the ironstone endemic *Melaleuca* aff *incana* (NG & ML 593). The long period of inundation well into the summer appears to restrict species richness in this community type, the only species group well represented is species group D and five species typical of winter wet swamps only occurred in this site (*Hakea linearis, Baumea juncea, Meeboldina scariosa* ms, *Meeboldina tephrina* ms, and *Platychorda applanata*). While all the ironstone communities have saturated soils during the winter and spring, only this community type is flooded to a depth of 30-50 cm for a period of several months each year.

Discussion

The high regional conservation values of the ironstone communities have been previously recognised (Anon 1990; Gibson *et al.* 1994; Smith & Ladd 1994; Robinson & Keighery 1997). More detailed work has shown that the Gingin, Busselton and Scott ironstone communities are floristically distinct and within those geographic areas further differentiation is possible which appears to be correlated with edaphic factors (particularly soil depth and clay content) as well as period of inundation. On the Scott Plain time since fire also appears to be significant since the dense shrublands of community type 8 appear to primarily differentiated from community type 4 by low occurrence of annual species.

Smith & Ladd's (1994) *Pericalymma ellipticum - Chamelaucium roycei - Grevillea diversifolia* association broadly covers the Busselton ironstones. They record only 48 species from five plots in their B2 group (mean richness 9.6 taxa per plot). This seriously underestimates the floristic diversity of this vegetation type. Our data records 236 taxa from 11 plots in this area (mean richness 21.5 taxa per plot), and average richness of the ironstone communities as a whole ranged from 14 to 67.9 taxa per plot with the richer community types being comparable with many upland heath communities. A significant component of this richness is the sequential germination and flowering of suites of annuals and geophytes (Appendix 1). This same pattern is seen in many of the clay-based wetlands on the coastal plain where high richness levels result from sequential groups of annuals that flower as the wetlands dry (personal communication, BJ Keighery & M Trudgen, DEP).

The ironstone vegetation types are a significant repository of biodiversity both in terms of high β-diversity and as a habitat for 20 restricted taxa. Of those 20 taxa 14 appear to be endemic to the ironstone substrate, while 12 are considered so seriously threatened as to be gazetted as Declared Rare Flora under the Wildlife Conservation Act 1950. The listing on this schedule is the strongest legislative protection that can be afforded to flora in Western Australia and requires Ministerial permission for any activity that may impact on these species in any way. A further seven taxa are presently being considered for gazettal (pers comm, K Atkins, CALM).

Many of these 20 taxa are still awaiting formal description or have only recently been described, indicating the incomplete state of knowledge of the flora of Western Australia even on the coastal plain within 200 km of the major population centre. Only eight of the 20 restricted taxa and five of the nine described community types are currently known from secure conservation reserves (National Parks or Nature Reserves).

The Gingin ironstone was always quite limited in area and the recent acquisition of the remaining block has conserved an estimated 50% of its original extent (Table 3). The Busselton ironstones have been the most heavily cleared for agriculture with only 3% of the original area remaining. The remnants are small and scattered and threatened by *Phytophthora cinnamomi* infection, inappropriate burning regimes and activities associated with mineral sands exploration and mining. One small remnant of *ca* 12 ha has recently been acquired as a conservation reserve while the acquisition of a second block of similar size is likely. While there are considerable areas of the Scott Plain's ironstone remaining as bushland most occurs on private property and very little occurs in secure conservation reserve (Table 3). Robinson & Keighery (1997) highlighted the importance of the recreation reserve immediately north of Scott River National Park for the conservation of the Scott Plain

Table 3

Estimates of original area, remaining uncleared area and percentage of the original in secure conservation reserve.

Area	Original area (ha)	Remaining uncleared area (ha)	%uncleared	% of original area reserved
Gingin	20	10	50	50
Busselton	2130	68	3	0.6
Scott Plain	1780	360	20	0.6

ironstone communities. Only unfavourable economic conditions of the early 1960s prevented a major iron ore mine being developed on the Scott Plains (see references in Baddock 1995).

Most of the areas of ironstone on the Swan and Scott Coastal Plains are clearly of Quaternary age (Tillie & Lantzke 1990; McArthur 1991; Baddock 1995) with the possible exception of ironstone deposits in Ironstone Gully near the base of the Whicher Range. Tille & Lantzke (1990) consider these of Quaternary age, while earlier mapping of nearby sections of the lower foot slopes of the Whicher Range indicate a Tertiary age (Belford 1987). This young age seems at variance with high level of endemism (13 taxa) seen on this substrate as well as the 50 km disjunction in distribution of several of the endemics between the Swan and Scott coastal plains (*Dryandra nivea* subsp *uliginosa*, *Calothamnus* aff *crassus*, *Chordifex isomorphus*, *Loxocarya magna*) and the 250 km disjunction of *Chordifex isomorphus*, *Hakea tuberculata* and *Lambertia orbifolia* between the Scott Plain and similar habitat in the Albany area. The absence of *Hakea tuberculata* between Scott River and Albany appears to relate to the lack of any ironstone formation in the intervening area. However, the reason for the absence of *Chordifex isomorphus*, *Lambertia orbifolia* and the endemics in seasonally wet lateritic areas on the Blackwood Plateau is not clear, but may be related to differences in chemical composition of the iron rich substrates (Anand 1998).

The evolution of the endemic flora of the ironstones may involve recent speciation events on the coastal plains after their deposition in the late Pleistocene, or much older speciation events from more widespread ancestral taxa with subsequent migration onto the ironstones of the coastal plain presumably in response to climatic change. Bousfield & James (1976) reported distinctive chromosome races for population of *Dampiera linearis* growing on the ironstones at the base of the Whicher Range compared with the diploid of the Blackwood Plateau and the tetraploid of the coastal plain but offer no suggestion of how old these chromosome races may be.

Given the present day distribution of the closest relatives of the ironstone endemics follow no consistent pattern, it is likely that the endemic species have a long evolutionary history. Four of the endemics are parapatric with their closest sister taxon, while 10 are allopatric, but separated by varying distances (one < 10 km, two between 10-50 km, one between of 50-100 km and four by more than 200 km). One endemic *Darwinia ferricola* ms has no close relative.

Of the 20 taxa whose distribution is centred on the ironstones, detailed phylogenetic and phylogeographic studies have only been undertaken for *Lambertia orbifolia* (Coates & Hamley 1999; Byrne *et al.* 1999). These studies, based on allozyme mating system, and chloroplast and nuclear rDNA analyses, indicate that a separation of the Scott Plain and Albany populations has occurred over an extended period of time in the evolutionary history of this species. Both these studies consider that genetic differentiation between these populations is such that the they should be recognised as separate conservation units.

If the phylogenetic pattern seen in *Lambertia orbifolia* is typical of the ironstone endemics then the local patterns of distribution now seen represent very recent migration onto the coastal plain of lineages with long and complex evolutionary histories.

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Appendix 1

Sorted two way table showing species occurrence by community type. Only taxa which occurred in at least two sites were included in the analysis. Columns represent individual sites with * indicating taxon occurrence at that site. Similar sites are classified into community types.

	COMMUNITY TYPE								
	1	2	3	4	5	6	7	8	9
SPECIES GROUP A									
Acacia extensa			*	*					
Darwinia oederoides	*			*					
Philotheca spicata				*	*				
Xanthosia huegelii				*	*				
Austrodanthonia setacea	*			** *					
Thysanotus tenellus	*			***					
Stylidium luteum subsp *glaucifolium*				**					
Caesia micrantha	*	*		* * *				*	
Chamaescilla corymbosa	**			* * *					
Burchardia multiflora	*		*	** *					
Homalosciadium homalocarpum				** * *		*			
Patersonia juncea				* *					
SPECIES GROUP B									
Acacia pulchella	**		*	***					
Aira caryophyllea	**		**	* * **					
Hyalosperma cotula	***			*** ***				*	
Siloxerus humifusus	** *			*** ***				*	
Patersonia occidentalis	*		*	*** ***	*			* *	
Podolepis gracilis				**** *				*	
Briza minor	***		*	* ** **				**	
Desmocladus fasciculatus	***	**	*	* ****				***	
Opercularia vaginata	***		**	* **		*		* **	
Xanthorrhoea preissii	*		**	* ****				*	
Aphelia cyperoides	****	***	* **	*******	*	*		** *	
Centrolepis aristata	****	**	****	* *****			*	* *	
Philydrella pygmaea	** *	**	* **	*** * *				** *	
Lepidosperma squamatum	*	*	****	*** * *		*		**	
Schoenus odontocarpus	* *		***	** * *			*		
Kunzea aff *micrantha* (BJK&NG 40)	***	**	****	*				*	
Drosera glanduligera	* **		* *	*** *					
Hemiandra pungens	***		* *	** **		*			
Hypochaeris glabra	****		****	****	*	*			
Phyllangium paradoxum	* *		***	****	*	*		*	
Cyperus tenellus	** *	*		***			*	****	
Lepyrodia aff *macra* (BJK&NG 1026)	**	*		** * *				*****	
Tremulina tremula	* **		*	** * *				**** *	
Loxocarya magna	***	*	***	*** *				**** *	
Pericalymma ellipticum	* **	***	****	* * *	*			*****	*
Stylidium ecorne	* *			* **			*	* ***	
Thelymitra flexuosa	***			** *				*	
Viminaria juncea	***	*	**	* *		*		*** *	
Drosera macrantha subsp *macrantha*	*		**	* * *					
Stylidium perpusillum	*			* *					
Hakea sp (BJK&NG 226)	*	***	* **	* * **					
Stylidium bulbiferum	**		* *	* * **		*			

Appendix 1 (continued)

	COMMUNITY TYPE								
	1	2	3	4	5	6	7	8	9
SPECIES GROUP C									
Desmocladus flexuosus			*					*	
Goodenia eatoniana	*		* *					*	
Hibbertia hypericoides			* *						
Dryandra nivea subsp *uliginosa*	*	**	*					*	
Vulpia bromoides		*	*	* *					
Laxmannia sessiliflora subsp *australis*	* **		**						
Stylidium repens	* **		**	*					
Millotia tenuifolia	*		**						
Pyrorchis nigricans	*		*						
Levenhookia pusilla	*		** *	*					
Thelymitra antennifera	*	*	****				*		
SPECIES GROUP D									
Astartea aff *fascicularis*				*				*	
Juncus bufonius		*		* *			*	*	
Cyathochaeta avenacea				* *				*	*
Melaleuca preissiana		*		* *					*
Meeboldina roycei ms				*					*
Melaleuca aff *incana* (NG&ML 593)				*					*
Eriochilus dilatatus	*			**					
Lolium rigidum				**					
Lepidosperma longitudinale				** *					
Melaleuca polygaloides				** *					
Poa poiformis				** *					
Grevillea manglesioides	*	*	*	*****					*
Stylidium inundatum	*			* **				*	
Hydrocotyle alata	*	*		** ***					
Tribonanthes australis				* **			*		
SPECIES GROUP E									
Centrolepis glabra				*			*		
Trithuria bibracteata				*			*		
Triglochin centrocarpum				* *			*		
Monopsis debilis	*	*		*			*	*	
Thysanotus multiflorus		*		*					
Hypolaena fastigiata				**					
Juncus articulatus				**					
Lotus suaveolens				***					
Isolepis cyperoides				**					
Leucopogon carinatus				* *					
SPECIES GROUP F									
Agonis flexuosa				*		*			
Boronia spathulata		*				*			
Hakea tuberculata				*		*		*	
Kunzea recurva				**		*	*		
Sowerbaea laxiflora				*		*			
Ornithopus compressus	*		* *			*			
Sonchus oleraceus			*			*			
Parentucellia viscosa			*	**		*			

Appendix 1 (continued)

	COMMUNITY TYPE								
	1	2	3	4	5	6	7	8	9
SPECIES GROUP G									
Amphipogon debilis				*				*	
Cassytha racemosa				* * *				*	
Isotoma hypocrateriformis				* *					
Bartsia trixago				* *					
Schoenus bifidus				* *					
Stylidium mimeticum	**	*		***					
Thelymitra crinita	*	*		*					
Thysanotus manglesianus	*			*					
Austrostipa compressa			*	* *					
Epilobium billardierianum			*	*					
Trichocline sp (BJK&NG 564)			*	*					
Conostylis setigera			*	*					
Neurachne alopecuroidea			***	*					
Selaginella gracillima	*		**	*					
Pimelea imbricata var *imbricata*			**						
Schoenus subflavus		*	**						
Stylidium crassifolium			**	*					
SPECIES GROUP H									
Acacia myrtifolia				* **				******	
Calothamnus aff *crassus* (R.D.Royce 84)				**** *	*			******	
Velleia trinervis			*	***** *				***	
Boronia anceps								*****	
Grevillea aff *manglesioides* (GJK 15158)								******	
Stenotalis ramosissima				*				******	*
Adenanthos detmoldii								**	
Chordifex isomorphus				*				** *	
Melaleuca incana								** **	
Caesia occidentalis						*		*	
Mesomelaena tetragona			*	* * *		*		**	
Vellereophyton dealbatum				* *		*		*	
Stylidium spathulatum				*	*			**	
Xanthorrhoea platyphylla								**	
SPECIES GROUP I									
Eutaxia virgata		*		*				*	
Schoenus rigens		*						*	
Hakea ceratophylla								*	*
Schoenus asperocarpus	*							*	
Sphenotoma capitatum					*			*	
Villarsia parnassifolia				*				*	
SPECIES GROUP J									
Actinodium cunninghamii			*		*				
Schoenus curvifolius			*		*				
Cytogonidium leptocarpoides		*			*				
Euchilopsis linearis		*			*				
Dasypogon bromeliifolius		*		*	*			* *	
Darwinia ferricola ms					*			**	
Cassytha glabella	*		**	*	*				
Drosera pallida				*	*				

Appendix 1 (continued)

	COMMUNITY TYPE								
	1	2	3	4	5	6	7	8	9
Dampiera linearis	**	**	*	**	*			*	
Baxteria australis				*	*				
Leucopogon pendulus	*			*					
Sphenotoma gracile				* *					
SPECIES GROUP K									
Acacia stenoptera	***	**							
Chamelaucium roycei ms	***	*							
Podolepis gracilis swamp form (GJK 13126)	* *								
Polypogon tenellus	* *								
Conostylis aculeata	**	*		*					
Isolepis oldfieldiana	*	*							
Calothamnus aff *quadrifidus* (BJK&NG 230)	*	*							
Patersonia occidentalis (swamp form)	*							*	
Thysanotus patersonii	*		*						
Briza maxima	***			*	*	*	*	*	
Romulea rosea	* *					*	*		
Haloragis tenuifolia	*			*			*		
Villarsia capitata	*						*		
Andersonia ferricola ms	* *		* *						
Drosera neesii	*		*						
Centrolepis drummondiana	**	*	**						
Lotus angustissimus	**		*						
Hypolaena pubescens	**			**				* *	
Microtis media	**			*				* *	
SPECIES GROUP L									
Borya scirpoidea	* **	* *	**						
Drosera rosulata	* **	* *					*		
Caladenia marginata	****	*		**					
Drosera menziesii subsp *menziesii*	* *	***		**					
Isolepis marginata	**	*		*			*		
Polypompholyx multifida	***	***	*	* *			*		
Elythranthera brunonis	*	*		*					
Stylidium obtusatum	*	*							
Drosera gigantea	*	*	**						
Stylidium calcaratum	* *	*	**						
Thysanotus thyrsoideus	*	**	**						
Hakea sulcata	*	*		*				** *	
Isopogon formosus subsp *dasylepis*	*	*							
Stylidium guttatum	*	*						*	
Caustis dioica	* *	***	**						
Chordifex sp		***	*						
Hypolaena exsulca	*	**	*		*				
Leptocarpus tenax	*	**							
Petrophile latericola ms	*	**							
Lyginia barbata		**						*	
Regelia ciliata		**							

Appendix 1 (continued)

	COMMUNITY TYPE								
	1	2	3	4	5	6	7	8	9
SPECIES GROUP M									
Adenanthos meisneri	*		*						
Hakea varia	*		*	*				*	
Stylidium pulchellum	**				*			*	
Chamaescilla corymbosa var *latifolia*			*					* *	
Hibbertia stellaris	*			*				* * *	
Nuytsia floribunda	*							*	
SPECIES GROUP N									
Angianthus preissianus	****								
Aphelia nutans	****								
Lepidosperma sp (BJK&NG 232)	***								
Siloxerus filifolius	* **								
Stylidium emarginatum	**								
Centrolepis alepyroides	* *							*	
Hydrocotyle callicarpa	* *			*					
Stylidium petiolare	* *								
Vulpia myuros	* *							*	
Centrolepis mutica	* **	*		***					
Verticordia plumosa	*	*		**					
Cicendia filiformis	*			*					
Juncus capitatus	* *			* *					
Schoenus discifer	* *	*		*					
Calothamnus lateralis	*	**		*					
Phylloglossum drummondii	* *	*							
Poa annua	*	*							
Dryandra squarrosa subsp *argillacea*	* *	*							
Utricularia violacea	*	*							
Tribonanthes violacea	**	*							
Crassula natans		*					*		

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Probability of grasstrees (*Xanthorrhoea preissii*) flowering after fire

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Abstract

Balga grasstrees (*Xanthorrhoea preissii* Endl) are widespread in south-western Australia, and flower profusely after fire. At five separate sites, the probability of flowering after fire was related to grasstree height, with tall plants more likely to flower than short ones. Height is probably a surrogate for age. We discuss the implications of this finding for both grasstree conservation and the reconstruction of fire history from grasstree flowering events.

Keywords: grasstree, fire history, phenology, *Xanthorrhoea*

Introduction

Grasstrees (*Xanthorrhoea* spp) are notable Australian plants due to their ubiquity, large size, unusual appearance, longevity, and spectacular flower spikes following fire. In south-western Australia the grasstree *X. preissii* is significant to the indigenous Noongar people, who call these grasstrees 'balga'. In the past, Noongars obtained many useful products from them, including gum, fish spears, fire drills, and edible 'bardi' grubs, *Bardistus cerberus* (Moore 1884). Grasstrees have a special place in Noongar folklore in connection with fire (personal communication, N Nannup, CALM).

Although grasstrees are still plentiful in south-western Australia, personal observations (DW) suggest that at long unburnt sites there is little regeneration, and old plants are dying without replacement. For example, Amphion Block, in state forest near Dwellingup, has been protected from fire since 1931. The stems of many grasstrees at Amphion are encased by termite mud, and the protective leaf bases are rotting in the damp conditions under the vast thatch. Although deaths directly attributable to rot and termite invasion have not yet been demonstrated, study is needed to determine the effect of long fire exclusion on grasstree health and reproduction. An understanding of the effect of fire on the survival, flowering and seed production of *Xanthorrhoea* is necessary for the conservation of this charismatic genus (Gill & Ingwersen 1976). Just as not all rare species are endangered, so not all common species are ultimately secure.

Due to their long life, high flammability, wide distribution, and stem structure, grasstrees may also give useful insights into local fire history (Lamont & Downes 1979; Ward 1996). Fire history, in turn, can give valuable insights into the role of fire in the recent evolution of Australian flora, fauna and ecological processes (Gardner 1955; Enright *et al.* 1998).

Methods

Cohunu Nature Park lies about 20 km south of Perth city, on the face of the Darling Scarp. In January 1994 a wildfire completely defoliated trees to 30 m above ground and most grasstrees were burnt. The stem height from soil to lowest green leaf, and the presence or absence of a flower spike were recorded for a sample of 500 grasstrees, located by random walking across the site, with each grasstree tagged as it was measured to prevent re-measurement. The random walk ensured that grasstrees of all heights had an equal chance of appearing in the sample.

A further four burnt sites were visited. These were Brady Block, on the Brookton Highway about 20 km from Karagullen (burnt summer 1995, visited 1996); Kangaroo Gully, also on the Brookton Highway, about 12 km from Karagullen (burnt autumn 1996, visited 1997); Ashendon Road near Mundaring (burnt spring 1997, visited 1998), and Crystal Brook Reserve near Kalamunda (burnt summer 1997, visited 1998). At each of these sites a sample of 500 grasstrees was measured and examined for evidence of recent flowering. The sample was random with regard to grasstree height. Taller and shorter trees had an equal chance of being included.

Abortion of some flower spikes due to attack by moth larvae of the genus *Meyriccia* (personal communication, T Burbidge, CALM) was noted at all sites. Although a careful search was made on each plant, it is likely that the shrivelled remnants of some flower spikes were missed, especially on very tall plants, or where the spike had aborted at a very early stage. In some cases the remnant may have disappeared altogether. Future investigators should be aware of the activities of this moth.

Firstly, the data from the five sites were split into flowering and non-flowering subsets to compare the height distribution within and between each sub-set. Mood's median test (Mood 1950) was used to test the null hypothesis of no height difference between flowering and non-flowering grasstrees. Mood's non-parametric test is less sensitive than the Kruskall-Wallis test, but more robust to outliers. In this case the height difference between the two groups was so large that sensitivity was not an issue, but there were a few unusually tall grasstrees.

The data were then recombined, sorted into height order, and split into sub-sets over the height range. For each site, this procedure gave 10 disjoint subsets of 50 observations each. For all sites pooled, the sorted heights were split into 50 disjoint subsets of 50 observations each. The median height (h) for each subset was compared with the proportion flowering (P) in that subset by a hemi-sigmoid model, where

$$\mathrm{P} = \tanh(\alpha + \beta^{*}h) \text{ for } (\alpha + \beta^{*}h \geq 0)$$

The parameters $\alpha + \beta$ of this hemi-sigmoidal model were obtained by linear regression of the metameter P with h;

$$P = \sqrt{(1+\mathrm{P})/(1-\mathrm{P})}$$

This is similar to, but in this case gave a better fit than, the well known logit metameter

$$P = \ln \sqrt{\mathrm{P}/(1-\mathrm{P})}$$

(Berkson 1944; Fisher & Yates 1957) which assumes the full sigmoidal model

$$\mathrm{P} = \{1 + \tanh(f)\}/2$$

(Emmens 1940).

Results

The height distributions of flowering and non-flowering grasstrees are shown for the data pooled over five sites in Fig 1. Each sampling site showed a very similar pattern, except that the grasstrees at some sites were generally taller than at others (Table 1). The height difference between grasstrees at the five sites is probably due to different growth rates resulting from varying site conditions. For example, the Crystal Brook site is dry, stony, and water shedding. Its grasstrees are small both in stem diameter (unpublished observations) and height, suggesting slow growth. Measurements (n = 100) of leaf-base deposition in the two years since the last fire gave an approximate mean growth rate of only 9 mm year^{-1}. Allowing 20 years before the stem starts vertical growth (BL, personal observation), the median age for flowering grasstrees at Crystal Brook was just over 80 years, and for non-flowering grasstrees was about 42 years. Kangaroo Gully, on the other hand, is a moist and water gaining site, with deep alluvial loam and outcropping granite. The growth rate estimated from leaf-base deposition since the fire was over 21 mm year^{-1}, so the median age for flowering grasstrees was just over 110 years, and for non-flowering grasstrees was about 58 years.

Table 1

Height of flowering and non-flowering grasstrees analysed by Mood's median test.

	Median Height (cm)			
	Flowering	Non-flowering	χ^2 value*	Significance**
Crystal Brook	57	20	64	<0.001
Cohunu Park	75	34	83	<0.001
Brady Block	104	40	101	<0.001
Ashendon Road	121	50	38	<0.001
Kangaroo Gully	190	80	151	<0.001
All sites pooled	97	47	290	<0.001

* 1 degree of freedom; ** Type I probability.

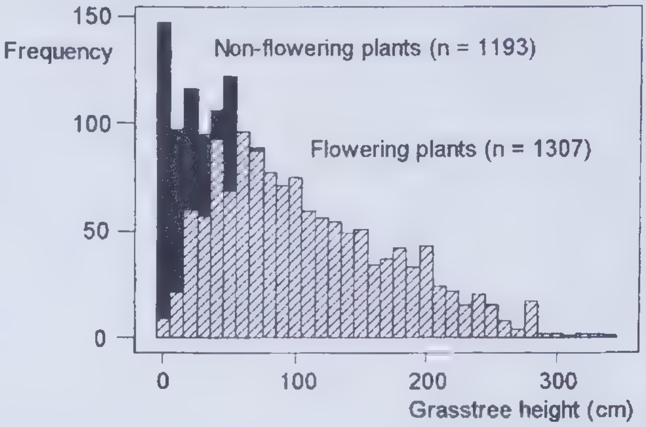

Figure 1. Frequency distributions for heights of flowering (light hatch, median = 97 cm) and non-flowering (dark hatch, median = 47 cm) grasstrees (all sites pooled).

The results of Mood's median test for grasstree heights at each site and for all sites pooled (Table 1) indicate that although the median height of both flowering and non-flowering grasstrees varies from site to site, we may conclude that there is a highly significant difference between the heights of flowering and non-flowering grasstrees at each site. The regressions used to fit the models are given in Table 2. The relationships between the probability of flowering and median grasstree height for each site, and for the pooled data, are shown in Fig 2.

Table 2

Parameters α and β for the fitted model $P = \tanh(\alpha + \beta^{*}h)$ obtained from linear regression of P and h; n = 10 for each sample and 50 for pooled sites.

	Regression	R^2	F	df	Significance*
Crystal Brook	$P = 0.258 + 0.013^{*}h$	0.929	104.2	1,8	<0.001
Cohunu Park	$P = 0.193 + 0.008^{*}h$	0.908	79.3	1,8	<0.001
Brady Block	$P = 0.124 + 0.007^{*}h$	0.916	87.3	1,8	<0.001
Ashendon Road	$P = -0.170 + 0.008^{*}h$	0.932	109.6	1,8	<0.001
Kangaroo Gully	$P = -0.294 + 0.007^{*}h$	0.873	54.9	1,8	<0.001
All sites pooled	$P = 0.190 + 0.006^{*}h$	0.851	274.5	1,48	<0.001

* Type I probability.

Discussion

Since taller grasstrees are more likely to flower than shorter ones, this study points to the importance of conserving taller grasstrees as a seed source. The role of tall grasstrees in this respect would be diminished if they were likely to die as a result of fire, as suggested by Curtis (1998). However, Taylor *et al.* (1998) did not observe any deaths among *X. fulva* after fire, and in this study several deaths apparently due to fire were only seen at one site (Brady Block) which experienced a fierce summer fire following a long period unburnt. Unlike

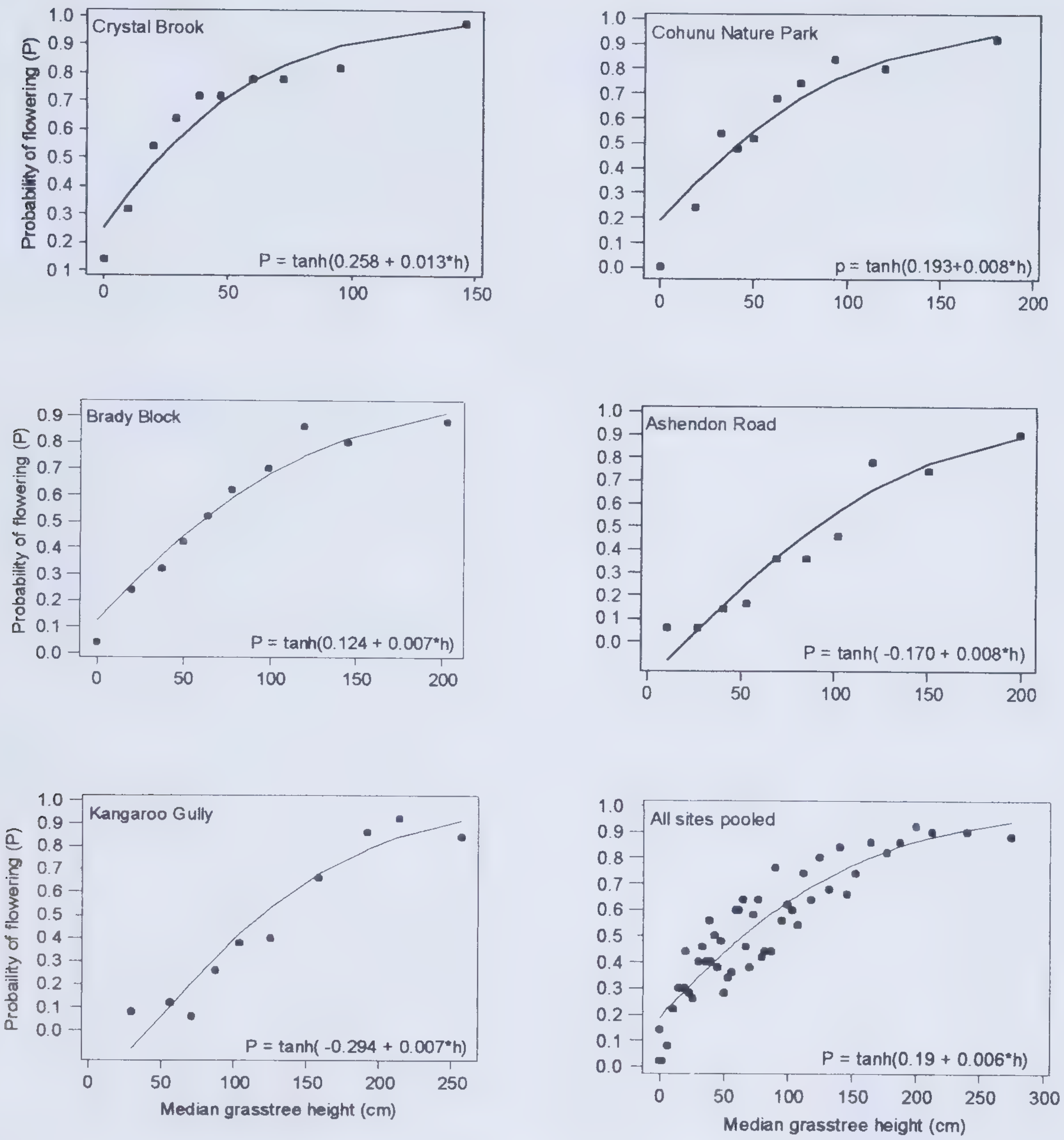

Figure 2. Models relating the probability of grasstree flowering to median grasstree height at five sites, and all sites pooled.

Curtis (1998), we did not find a general minimum height for flowering. At Crystal Brook, about 20% of plants flowered before their stems had emerged from the ground. However, at two sites (Kangaroo Gully and Ashendon) few flowered before the stems were 20 cm tall.

It has been suggested that short inter-fire intervals encourage flowering in *X. fulva* (Taylor *et al.* 1998). It also seems likely that frequent, light burning would protect old grasstrees from fierce, potentially lethal, fires which occur when thatch is allowed to build up over long periods. By promoting flowering, frequent burning would also promote seed production. Recent research into fire marks on grasstrees in south-western Australia suggests that, before European settlement, most were burnt every 3 to 4 years (Ward & Sneeuwjagt 1999).

Previous workers (Lamont & Downes 1979) used the growth rate and flowering history of grasstrees to reconstruct fire history back to pre-European times. Flowering events were identified by flower spike remnants close to swerves or forks in the stem. Since grasstrees usually have straight stems for the first metre or so above ground, with no evidence of flowering, it was concluded that fire frequency at the site examined was lower before European settlement than after. Our results now show that flowering history is an unreliable surrogate for fire history, due to the lower probability of flowering in shorter plants. Also, longitudinal sections of stems have shown that spike remnants are often engulfed by secondary growth of the stem, so that flowering events may be missed by external examination (BL, personal observation).

While grasstrees sometimes flower without the stimulus of fire, it is a common observation that fire causes prolific flowering (Specht *et al.* 1958; Baird 1977; Lamont & Downes 1979). Ethylene gas in smoke has been suggested as a flowering stimulus (Gill & Ingwersen 1976) although their results were equivocal. In this study it was noted that grasstrees outside the burnt area, but close enough to have been affected by smoke, sometimes flowered (also see Curtis 1998). A study of the effect of smoke on grasstrees stratified by height might give a clearer result.

Acknowledgements: We thank T Burbidge for identification of the moth larvae, and information on their habits. We thank biology students of Curtin University for their efforts in collecting field data, and M Williams of the Department of CALM for correcting one of us (DW) on the logit transformation.

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Monitoring aquatic invertebrates and waterbirds at Toolibin and Walbyring Lakes in the Western Australian wheatbelt

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Abstract

Toolibin and Walbyring Lakes are adjacent wetlands in the Western Australian wheatbelt, a region with widespread secondary salinization. Salinity of water in Toolibin has increased in recent years and a Recovery Plan is being implemented to reduce salt loads; Walbyring is also threatened by salinization. As part of a monitoring program to evaluate success of recovery actions, waterbirds and aquatic invertebrates were sampled at both wetlands in December 1996. Toolibin Lake had the richer waterbird community, while Walbyring Lake contained more invertebrate species. Results suggested that gross changes in wetland communities can be detected by monitoring based on an annual waterbird survey and a pair of invertebrate samples collected with 110 µm and 250 µm-mesh pondnets. Comparison of waterbird data from Toolibin in 1996 with earlier surveys showed increases in salinity to 1996 affected occurrence of only a few species. Comparison of invertebrate data from both wetlands in 1996 with surveys in 1992 provided little evidence that increased salinities affected invertebrates, other than water mites. It is suggested that the freshwater fauna of the wheatbelt is comparatively salt-tolerant and substantial changes in community composition will be seen only when salinities exceed 10 000 mg L^{-1}.

Keywords: aquatic invertebrates, waterbirds, monitoring, salinity, wetland, monitoring

Introduction

Toolibin and Walbyring Lakes, approximately 40 km east of Narrogin in the wheatbelt region of south-west Western Australia, are part of a series of seasonally or intermittently flooded wetlands forming the headwaters of the Arthur River, which then flows into the Blackwood River. For many years, the two wetlands were popular duck-hunting sites but Toolibin was closed to hunting in 1974 and Walbyring in 1992. Since then, management has been focused on conservation values of the wetlands (Northern Arthur River Wetlands Committee 1987; Froend *et al.* 1997). Toolibin (296 ha) is larger than Walbyring (53 ha) but they are superficially similar. Both support extensive stands of *Casuarina obesa* and *Melaleuca* trees across the lake-bed as well around the shoreline (Froend *et al.* 1987; Halse *et al.* 1993a), although stands are better developed at Toolibin and were one of the justifications for it being listed in 1990 as a Wetland of International Importance under the Ramsar Convention (Froend *et al.* 1997). Another justification was the waterbird community at Toolibin. Up to 1995, 49 waterbird species had been recorded, with evidence of breeding by 25 species (Froend *et al.* 1997). Doupé & Horwitz (1995) also found what appeared to be, in the absence of comparative data from other wheatbelt wetlands, a rich invertebrate fauna at Toolibin, as well as Walbyring, and suggested that regular sampling of aquatic invertebrate assemblages could be an effective way of monitoring ecological condition of these wetlands.

Secondary salinization is probably the most serious threat to conservation of wetland biota in the Western Australian wheatbelt (see Williams 1987). Over the past 60 years, almost all wetlands in the region have become saline, with resultant death of trees that initially grew on the lake-bed or low on the shoreline (Halse *et al.* 1993a). Toolibin and Walbyring are exceptional in that they have remained comparatively fresh, perhaps because of unusual hydrogeology. Nevertheless, salinity is increasing at Toolibin and, to a lesser extent, at Walbyring and the biological communities at both are now threatened (Froend *et al.* 1997). To reduce the threat at Toolibin, land on the western side of the lake was bought for conservation purposes and planted with trees in 1988. In addition, drainage in the catchment was altered to reduce the salinity of surface water flowing into the lake, and groundwater pumps were installed to lower the water-table beneath it (Halse 1988; Hooper & Wallace 1994). A Recovery Plan recommended that, in association with these recovery actions, biological attributes of Toolibin should be monitored because they are the reason the lake is being conserved and provide the ultimate measure of success of recovery actions (unpublished report, R Froend & A Storey, Department of Conservation and Land Management, 1996).

Two biological attributes recommended for monitoring are waterbirds and aquatic invertebrates. It was proposed that Walbyring be sampled as well as Toolibin because, in recent years, it has been the fresher of the two wetlands (unpublished data, J A K Lane, Department of Conservation and Land Management) and Doupé & Horwitz (1995) found it contained more species of aquatic invertebrates. This paper presents results of waterbird and invertebrate monitoring in December 1996 with three objectives. First, to provide data on condition of the two wetlands in 1996. Toolibin has long been recognised as having high conservation values and being worthy of management intervention to maintain these values (Halse 1988; Hooper & Wallace 1994). It may serve as a useful benchmark when assessing conservation values of other wheatbelt wetlands. Second, to evaluate whether the monitoring methodologies reliably characterised faunal communities of the wetlands and enabled changes in ecological character to be recognised. Third, to examine whether increased salinity has altered waterbird and aquatic invertebrate communities at Toolibin and Walbyring.

Methods

After drying during the previous summer, Toolibin and Walbyring flooded in July 1996 and retained water in early December 1996. Waterbirds were surveyed by GBP on foot and by canoe on 4 December 1996. Binoculars and a spotting scope were used and comprehensive waterbird counts were obtained for both wetlands. Incomplete waterbird surveys were made by SAH on 18 December 1996 by scanning with a spotting scope from various sectors of the wetlands while sampling invertebrates.

Aquatic invertebrates were sampled on 18 December. Three pairs of samples (each pair constituting one replicate) were collected from different sectors of Toolibin (Fig 1) to maximise the range of habitats sampled, using pond-nets with mesh sizes of 110 µm and 250 µm. Each replicate consisted of 50 m of sweeping through the water column, submerged vegetation, bottom sediments and scraping past logs and tree trunks with the 250 µm-mesh pond-net and 20 m of sweeping for zooplankton with the 110 µm-mesh pond-net. The 250 µm-mesh sweeps were not continuous; they were collected over a distance of about 200 m. In Walbyring, 250 µm-mesh sweeps were collected from three sectors but a matching 110 µm-mesh zooplankton sample was taken only in sector 2 (Fig 1).

Invertebrate samples were immediately preserved in 70 % alcohol and returned to the laboratory for sorting. In the laboratory, each 250 µm-mesh sample was washed and larger pieces of organic debris were removed before the sample was poured through three sieves with 2 mm, 500 µm and 250 µm mesh size. The portion of the sample retained in each sieve was sorted under a dissecting microscope and all taxa were identified to the lowest level possible (usually species). The 110 µm-mesh samples were sorted without sieving.

In each sector of Toolibin where invertebrates were sampled, conductivity, pH, dissolved oxygen and temperature were measured *in situ* with a WTW Multiline P4 meter and water samples were collected for laboratory measurement of total dissolved phosphorus, total dissolved nitrogen, chlorophyll *a,b,c* and phaeophytin. Extra samples were collected in the eastern sector to determine total dissolved solids (TDS) by gravimetry, ionic composition, colour and turbidity. Analytical methods described by Eaton *et al.* (1995) were used. At Walbyring, water quality parameters were measured only in sector 2.

Analysis

Long-term trends in salinity at Toolibin were examined using depth and salinity data collected two-monthly between 1981-85, and each September and November subsequently, by J A K Lane at the Department of Conservation and Land Management depth gauge (Lane & Munro 1983; unpublished data, J A K Lane, CALM).

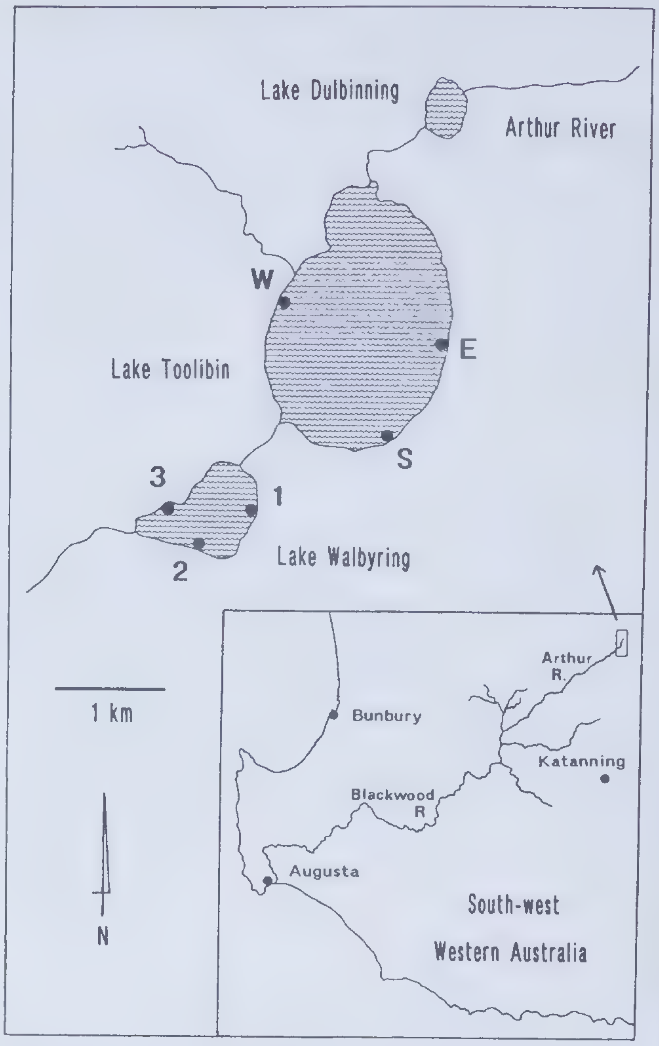

Figure 1. Sectors sampled for invertebrates at Toolibin and Walbyring Lakes on the Northern Arthur River, south-western Australia, and connection of the lakes with the Blackwood River.

Long-term changes in the waterbird community at Toolibin were examined using the December 1996 surveys and six previous spring (August-October) surveys identified by Froend *et al.* (1997) as representing pre-salinization (combined data from surveys between 1965-74) and current baseline (1975, 1981-84) communities. The 1990 survey that Froend *et al.* (1997) designated as current baseline was an outlier (see Fig 4 in Froend *et al.* 1997) and was omitted from analyses. Relationships between number of species recorded and calendar year or salinity at time of survey were examined by correlation analysis. The relationship between surveys, in terms of species composition, was examined firstly by classifying surveys, using unweighted pair group arithmetic averaging in the PATN analysis package with presence/absence waterbird data, the Czekanowski association measure and a β-value of -0.1 (Belbin 1993). Presence/absence data were used because the composite pre-salinization survey represented a species list rather than reliable counts. Secondly, surveys were plotted on an ordination using semi-strong-hybrid multi-dimensional scaling with orthogonal axis rotation.

The ability of single surveys to distinguish waterbird communities of different wetlands, in an ordination, was examined by including data from Walbyring and earlier surveys of Lakes Chandala, Cooloongup and Eganu and a small wetland on the eastern side of Watheroo National Park in the ordination of Toolibin surveys. Chandala, a freshwater wetland with *Melaleuca rhaphiophylla* trees growing across the lake-bed, and Cooloongup, a shallow saline wetland with freshwater seeps and extensive sedge beds, are on the Swan Coastal Plain and were surveyed in October 1990 and 1991 (Storey *et al.* 1993a). Eganu, formerly a *Casuarina obesa/Melaleuca* wetland and now severely salinized, and the Watheroo wetland, a brackish *Casuarina obesa* wetland in which water levels have risen markedly over the last 20 years (see Halse 1981), were surveyed during November 1989 and 1991 (unpublished data, S A Halse).

For invertebrate sampling, the amount of fidelity shown by replicates to composite samples in a classification of Toolibin and Walbyring invertebrate data was used to evaluate whether one replicate (a single pair of 250 µm and 110 µm sweeps) adequately characterised the invertebrate communities of the two wetlands. Composite samples comprised all taxa collected in the three replicates for each wetland. The classification was done using unweighted pair group arithmetic averaging, presence/absence data, the Czekanowski association measure and a β-value of -0.1. Sampling effort was slightly lower in the two Walbyring replicates without 110 µm-mesh samples (sectors 1 and 3) than other replicates.

Whether single replicates were likely to detect gross changes in the invertebrate communities of Toolibin and Walbyring was examined by ordinating data from the two lakes with data from Chandala, Cooloongup and a small wetland near Gingin. These three wetlands were sampled in October-November 1989 and 1990 by randomly taking six 10 m sweeps with a 250 µm-mesh pondnet from around the wetland margin (Davis *et al.* 1993). Semi-strong-hybrid multi-dimensional scaling with orthogonal axis rotation was used. Replicates were not compared with earlier data from Toolibin and Walbyring (Doupé & Horwitz 1995), to examine whether communities had changed over time, because of very substantial differences in sampling methodology.

Adequacy of the invertebrate sampling methods employed at Toolibin and Walbyring, in terms of providing a complete species list for the taxa identified, was assessed using the equation of Kay *et al.* (1999) to estimate total numbers of invertebrate species present in each wetland, and number of replicates required before another collected fewer than one extra species;

$$a_i = a_{i-1} \times (a_3/a_2)$$

where a_i was the average number of additional species collected in the i^{th} replicate and a_2 and a_3 were the average number of additional species collected in the second and third replicates, respectively.

Results

Water chemistry

Maximum water depths on 4 December 1996 were about 0.8 m at Toolibin and Walbyring. Depths were reduced by about 0.1 m on 18 December 1996 (Table 1), when salinity at Toolibin varied from 9400 mg L^{-1} TDS on the eastern side to about 12 500 mg L^{-1} (estimated from conductivity, see Table 1) on the more saline western side. Walbyring had a salinity of 2800 mg L^{-1} TDS. Ionic composition of both wetlands was dominated by sodium chloride. Levels of nutrients and chlorophyll in Toolibin were low and differences between sites were small. There was a mild algal bloom in Walbyring (Table 1). Salinities measured at Toolibin during previous waterbird surveys between 1975 and 1990 varied from 960-3800 mg L^{-1} TDS; maximum depth was 0.8 m in 1975 and 1988 and ranged

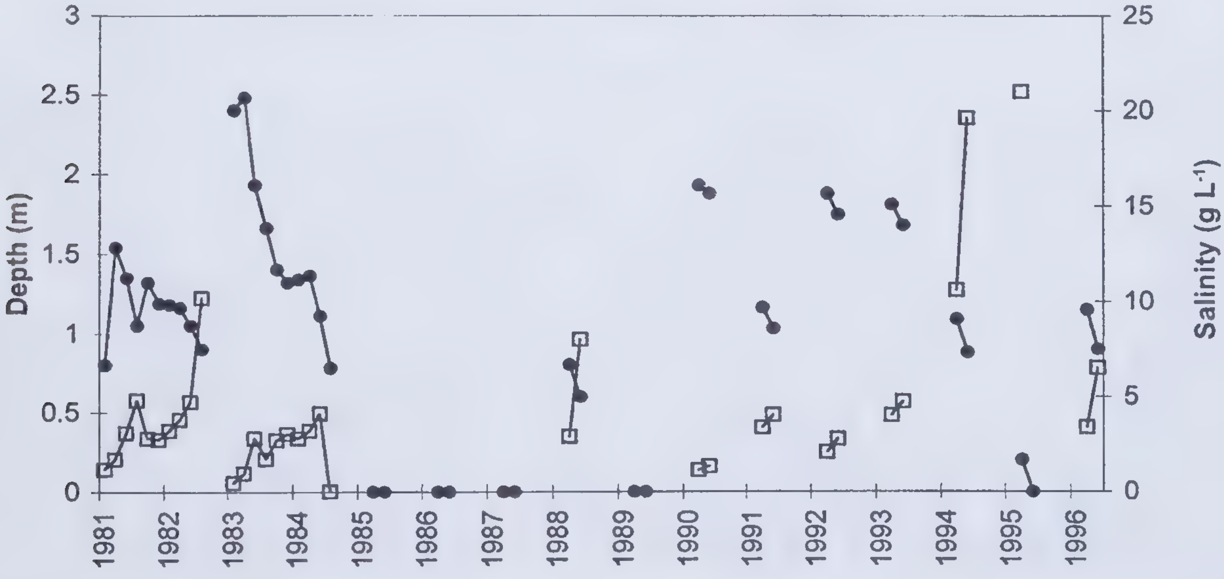

Figure 2. Depth (●) and salinity (□) at Toolibin Lake at 2-monthly intervals from July 1981 to May 1995 and each September and November thereafter (unpublished data, J A K Lane, Department of Conservation and Land Management), except in 1996 when December data are used instead of November (modified from Froend *et al.* 1997)

Table 1

Chemical and physical measurements of water in sectors of Toolibin and Walbyring Lakes on 18 December 1996 (see Fig 1 for location of sectors).

	Toolibin East	Toolibin South	Toolibin West	Walbyring 2
Lake Depth (m)	0.66			0.74
pH	7.0	7.1	7.0	6.9
Dissolved Oxygen (%)	217	217	215	154
Temperature (°C)	32	31	26.5	27
Colour (TCU)	54			89
Turbidity (NTU)	1.2			66
Total Dissolved Solids (mg L^{-1})	9400			2800
Conductivity (mS m^{-1})	1520	1690	2020	470
Alkalinity (mg L^{-1})	95			220
Ca^{2+} (mg L^{-1})	280			78
Mg^{2+} (mg L^{-1})	380			81
Na^{+} (mg L^{-1})	2800			800
K^{+} (mg L^{-1})	47			23
CO_3^{2-} (mg L^{-1})	<2			<2
HCO_3^{-} (mg L^{-1})	120			280
Cl^{-} (mg L^{-1})	5300			1300
SO_4^{2-} (mg L^{-1})	570			74
SiO_2 (mg L^{-1})	4.0			14
Total Dissolved Nitrogen (mg L^{-1})	4.2	3.6	4.0	3.0
Total Dissolved Phosphorus (mg L^{-1})	0.01	0.01	0.01	0.03
Chlorophyll *a,b,c* (mg L^{-1})	0.003	0.001	0.006	0.036
Phaeophytin (mg L^{-1})	<0.001	<0.001	<0.001	0.007

Table 2

Counts of waterbird species recorded at Toolibin and Walbyring Lakes in December 1996.

		Toolibin 4.xii.96	Toolibin 18.xii.96	Walbyring 4.xii.96	Walbyring 18.xii.96
Blue-billed duck	*Oxyura australis*			2	
Musk duck	*Biziura lobata*			6	4
Freckled duck	*Stictonetta naevosa*	1	25	33	
Black swan	*Cygnus atratus*	1	2	1	
Australian shelduck	*Tadorna tadornoides*	74	97	5	57
Australian wood duck	*Chenonetta jubata*	8		20	20
Pacific black duck	*Anas superciliosa*	17	3	44	1
Australiasian shoveler	*Anas rhynchotis*	4	56	8	
Grey teal	*Anas gracilis*	194	1162	430	367
Pink-eared duck	*Malacorhynchus membranaceus*	154	134	300	8
Hardhead	*Aythya australis*	25	60	36	58
Hoary-headed grebe	*Poliocephalus poliocephalus*	14	1	28	22
Little pied cormorant	*Phalocrocorax melanoleucos*	10	1		
Great cormorant	*Phalocrocorax carbo*	1			
White-faced heron	*Ardea novaehollandiae*	5	2	6	
White-necked heron	*Ardea pacifica*	2	1		
Great egret	*Egretta alba*		1		
Nankeen night heron	*Nycticorax caledonicus*	5			
Yellow-billed spoonbill	*Platalea flavipes*	26	2	1	4
Dusky moorhen	*Gallinula tenebrosa*			1	2
Eurasian coot	*Fulica atra*	201	281	6	12
Marsh sandpiper	*Tringa stagnatilis*	1			
Black-winged stilt	*Himantopus himantopus*	51	19		
Red-kneed dotterel	*Erythrogrys cinctus*	60	11		
Unidentified shorebird[1]			1		
Number of birds		**854**	**1859**	**927**	**555**
Number of species		**20**	**18**	**16**	**11**

[1] Probably a Marsh Sandpiper but excluded from the ordination.

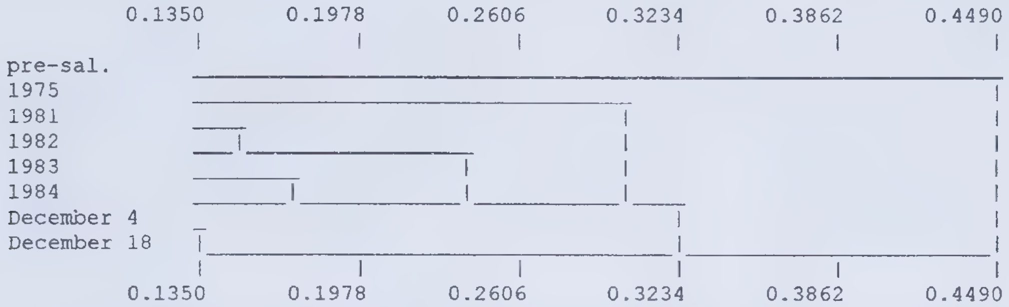

Figure 3. Classification of 8 waterbird surveys at Toolibin Lake, based on species composition. The pre-salinization survey contains composite data from 1965-74 and the December surveys were conducted in 1996.

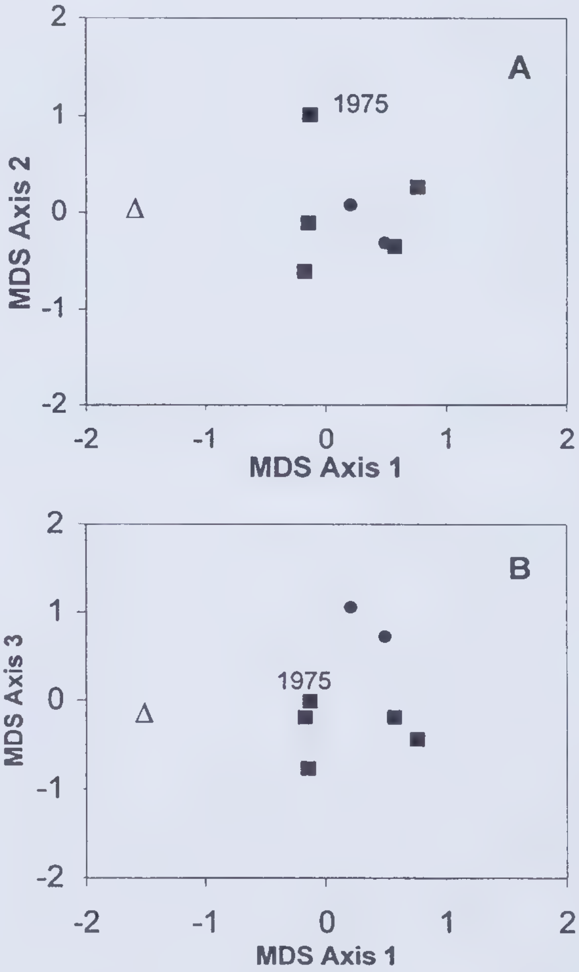

Figure 4. Three-dimensional ordination of 8 waterbird surveys from Toolibin Lake, based on species composition, showing relative positions of pre-salinization (Δ), baseline (1975, 1981-84, ■) and 1996 surveys (●); stress = 0.10.

from 1.2-2.0 m during other surveys (unpublished data, J A K Lane, CALM).

Between 1993 and 1995, salinity levels in Toolibin increased compared with the previous 12 years (Fig 2). This trend lessened in 1996 after the installation of a separator on the inflow channel so that only fresh water flowed into the lake. Toolibin did not overflow into the Arthur River and, therefore, export salt, between 1993 and December 1996 (unpublished report, R Froend & A Storey, Department of Conservation and Land Management, 1996).

Waterbirds

A total of 854 waterbirds of 20 species were recorded at Toolibin on 4 December 1996, and 1858 waterbirds of 17 species were recorded on 18 December 1996. Equivalent counts at Walbyring were 927 waterbirds of 16 species on 4 December, and 555 waterbirds of 11 species on 18 December (Table 2). Assuming the unidentified pale sandpiper-like shorebird seen at Toolibin on 18 December was a marsh sandpiper, all but three species recorded on 4 December were seen during the second survey. One additional species, the great egret, was seen.

The most interesting waterbird sightings were freckled ducks at Walbyring on 4 December and Toolibin on 18 December, the marsh sandpiper at Toolibin on 4 December and dusky moorhens at Walbyring during both surveys (Table 2). Marsh sandpipers have not been recorded previously at Toolibin, although they are quite common around fresh and brackish wetlands in south-western Australia (Jaensch *et al.* 1988), and the sighting increased the species list for Toolibin to 50. Similarly, dusky moorhens have not been recorded previously at Walbrying or Toolibin. Freckled ducks occur regularly at Toolibin, with 600 being recorded in 1981 (Jaensch *et al.* 1988) and several hundred in 1960 (see Froend *et al.* 1997), but the count of 25 on 18 December represented a significant concentration in south-western Australia (Halse *et al.* 1995). The 33 freckled ducks seen at Walbyring on 4 December were probably the same flock as seen at Toolibin two weeks later.

Numbers of waterbird species recorded at Toolibin each survey were not significantly correlated with calendar year (r = -0.58, n = 8, P = 0.13) or salinity at the time of survey (r = -0.37, n = 8, P = 0.48), assuming the pre-salinization salinity was 1000 mg L^{-1}. The largest differences in community composition were between the pre-salinization and subsequent surveys (Figs 3 & 4). This may be partly artefactual because the pre-salinization survey was created by combining records from many small surveys between 1965-74 and comprised a number of species (37) that was higher than likely to be seen in any single survey either pre- or post-salinization. A "post-salinization survey" created by combining the 7 surveys between 1975-96 would have recorded a similar number of species (35). Nevertheless, 11 species recorded pre-salinization were not recorded in subsequent surveys and 9 species recorded post-salinization were not

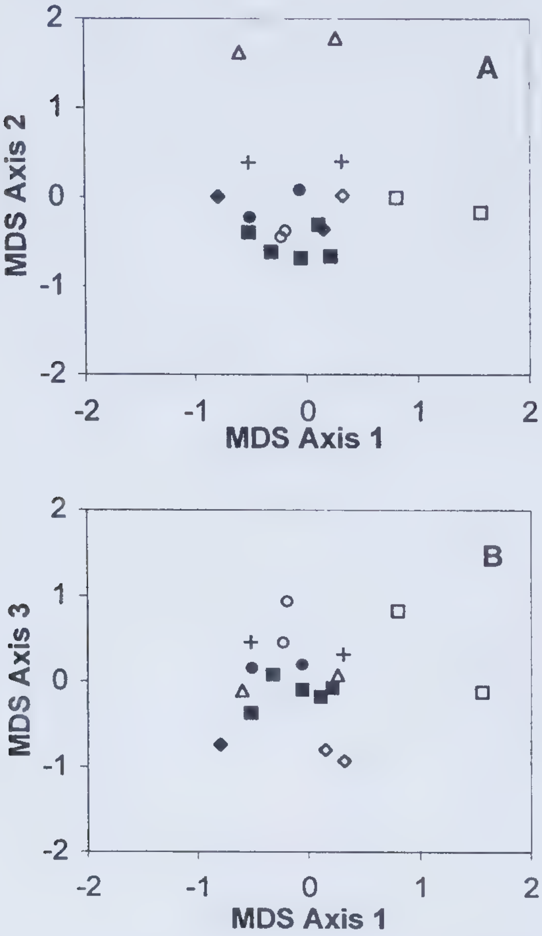

Figure 5. Three-dimensional ordination of waterbird surveys from Toolibin Lake (presalinity, ◆; baseline, ■; 1996, ●), Walbyring Lake (○), Lake Chandala (◇), Lake Cooloongup (△), Lake Eganu (□) and a small wetland (+) on the eastern edge of Watheroo National Park (see text for details), showing separation of Eganu, Cooloongup and Chandala from the other, *Casuarina obesa*-dominated wetlands; stress = 0.14.

recorded earlier. Some of these differences may have resulted from sampling error but the post-salinization disappearance from Toolibin of species with strong preference for fresh water, such as Australasian bitterns and purple swamphens, appears to have been a real response to salt-induced habitat change at the lake (Froend *et al.* 1997).

Although grouped together by Froend *et al.* (1997), the 1975 and early 1980s baseline surveys had slightly different waterbird communities (Figs 3 & 4). Further change was observed in 1996, suggesting that a series of changes have occurred in the waterbird community at Toolibin over the last 30 years. Species that were common in pre-salinization and baseline surveys but absent from 1996 were musk ducks (all earlier surveys), great crested grebes (five-sixths of surveys), Australasian grebes (two-thirds), blue-billed ducks and little black cormorants (half). None of these species commonly occur in very saline water and, other than little black cormorants, rarely occur at salinities >10 000 mg L^{-1} (see Jaensch *et al.* 1988; Halse *et al.* 1993b).

Compared with the large differences between wetland types, changes in the waterbird community at Toolibin have been relatively small (Fig 5). The waterbird community of Toolibin was readily distinguished from that of the *Melaleuca*-dominated Chandala, heavily salinized Eganu and sedge-lined Cooloongup. The communities of Walbyring and Watheroo, both *Casuarina obesa* wetlands in the early stages of salinization, were fairly similar to Toolibin. Prior to salinization, Eganu contained extensive stands of *Casuarina obesa* and *Melaleuca* sp and its waterbird community probably gives an indication of what will occur at Toolibin (and Walbyring and Watheroo) if salinization continues.

Aquatic invertebrates

A total of 83 species of aquatic invertebrate were collected on 18 December, with 52 and 63 species recorded in Toolibin and Walbyring, respectively (Appendix). Rotifers were present but were poorly collected because mesh sizes were too large. Fauna in the sweeps was dominated by insects (65 % of species), with crustaceans accounting for another 28 %, annelids 5 % and molluscs 2 %. Beetles (28 % of insect species) and chironomids (19 %) were the major groups of insects, while ostracods (43 %) were the main group of crustaceans. Nearly all species collected were widespread fresh or brackish water taxa, although some halophilous species occurred in the sweep on the western side of Toolibin, including the beetle *Necterosoma penicillatus* (see Halse 1981) and ostracod *Mytilocypris tasmanica chapmani* (see De Deckker 1983).

Three replicate invertebrate samples provided fairly complete species lists at Toolibin and Walbyring for the taxa that were identified (Fig 6). Between 4 and 5 replicates (95 % confidence limits) were required at Toolibin before another would collect, on average, < 1 extra species (*i.e.* the species list would be almost complete); between 4 and 6 were required at Walbyring. Proportion of the invertebrate fauna in each wetland collected by individual replicates varied from 69-80 %, with three replicates collecting, on average, 92-93 % of the fauna. All replicates appeared sufficiently comprehensive to characterize the wetland from which they were collected (Fig 7), although small dissimilarities occurred between the replicate from the more saline

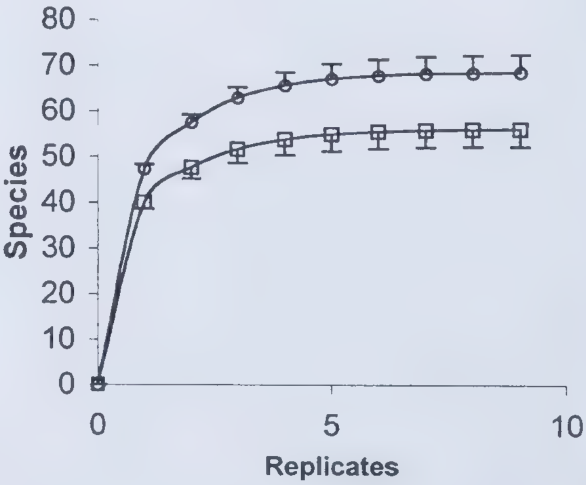

Figure 6. Accumulation of invertebrate species at Toolibin (□) and Walbyring (O) Lakes with increasing numbers of replicates (see text for details); error bars are ± 1 SE.

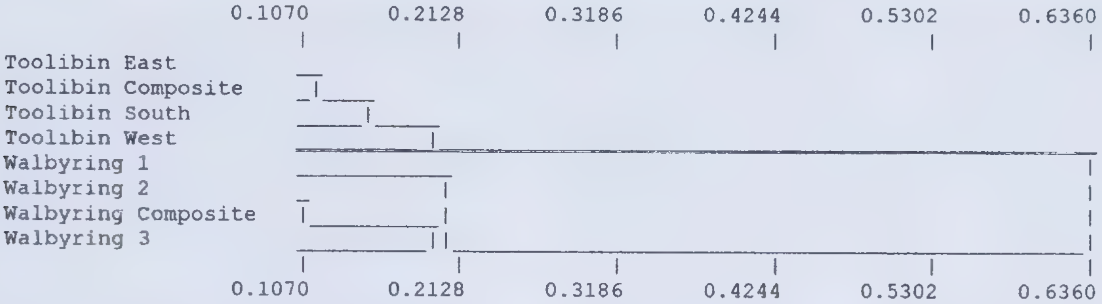

Figure 7. Classification of replicates and composite samples from Toolibin and Walbyring Lakes, showing the similarity of replicates from the same wetland.

western sector of Toolibin and other Toolibin replicates and between the Walbyring replicate from sector 2, at which 3 extra species were collected in the 110 µm-mesh sweep (Appendix), and other Walbyring replicates. When samples from three wetlands on the Swan Coastal Plain (Chandala, Cooloongup and Gingin) were included with Tolibin and Walbyring in a classification, all wetlands were separated clearly, with replicates from Toolibin and Walbyring clustering close to the composite sample of the respective lake (Fig 8).

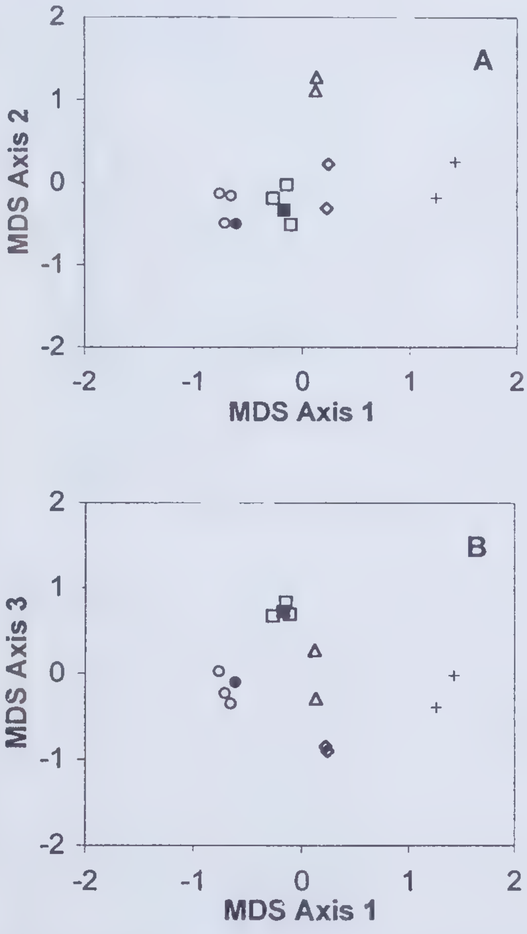

Figure 8. Three-dimensional ordination of invertebrate replicates and composite samples from Toolibin (□) and Walbyring (O) Lakes, Lake Chandala (◇), Lake Cooloongup (Δ), and 2 samples from a small wetland near Gingin (+) for different years (see text for details), showing discrimination between wetlands and proximity of replicates to the composite samples (filled symbols); stress = 0.09.

Discussion

Surveys of south-western Australian wetlands in the early 1980s showed Toolibin to be among the 10% of wetlands supporting most waterbird species (Jaensch *et al.* 1988; Halse *et al.* 1993b). The 20 species recorded at Toolibin on 4 December 1996 reflected this high waterbird conservation value. Toolibin provides an excellent benchmark against which to assess waterbird conservation value of other wetlands because its use by, and value to, waterbirds is widely accepted and management responses are well documented (Halse 1988; Hooper & Wallace 1994; Froend *et al.* 1997).

This study collected more invertebrate species at Toolibin than Doupé & Horwitz (1995) collected in October 1992 (52 *vs* 36) because sampling and sorting effort was greater and probably provides a better estimate of the conservation value of the lake. With 52 species in 1996, Toolibin appeared to have moderate invertebrate conservation value, based on species richness, although comparisons with other wetlands may be confounded by differences in sampling effort (see Fig 6). Five wheatbelt wetlands sampled in October 1997, with similar methodology but about 50% more effort than Toolibin, had 20-87 invertebrate species (mean 51 ± se 11) (unpublished data, S A Halse). With six 10 m sweeps using a 250 µm mesh pond-net, Davis *et al.* (1993) recorded 12-66 species (mean 35 ± se 2) in a single spring sampling of 40 wetlands on the Swan Coastal Plain. Storey *et al.* (1993b) recorded 36-70 species (mean 57 ± se 10) in February in three wetlands at Two Peoples Bay in the wet south-west corner of Western Australia with similar methodology, but about half the sampling effort, of this study.

Judged by species richness, Walbyring appeared to have greater invertebrate conservation value than Toolibin during this study (Appendix). Doupé & Horwitz (1995) also found higher invertebrate species richness per unit sampling effort at Walbyring. Neither lake is particularly satisfactory as a benchmark against which to compare the conservation value of other wetlands for invertebrates, because their species richness is intermediate and the management implications of their invertebrate lists are unclear.

Both the waterbird and invertebrate survey methodologies used in this study produced results that could be used to characterise wetlands. Despite the waterbird survey of Toolibin on 18 December being rather cursory and undertaken two weeks after the more thorough survey of 4 December, species composition was similar and surveys occupied similar positions in ordination space (Figs 4 & 5). Walbyring was also characterised adequately, despite either substantial changes in species composition between surveys or some species being overlooked on 18 December. Both sets of surveys confirmed the long-term pattern of greater waterbird richness at Toolibin than Walbyring (Jaensch *et al.* 1988) and clearly separated Toolibin and Walbyring from wetlands without extensive living *Casuarina obesa*.

Froend *et al.* (1997) proposed that ordination could be used to track changes in wetland communities through time and results from Toolibin suggest this can be done for waterbirds using a single survey each year (Figs 4 & 5). There are some important considerations, however, that apply to monitoring both waterbirds and invertebrates. Firstly, numbers and species of waterbirds and invertebrates using a wetland fluctuate seasonally and annually accordingly to wetland conditions (Gosper *et al.* 1983; Halse *et al.* 1992; Davis *et al.* 1993), so inter-annual comparisons should be restricted to the same season in years with roughly similar wetland depths. Secondly, sampling errors may be large owing to changes in species composition during the day of survey (mostly a problem with waterbirds), species being overlooked by the survey, collecting and sorting techniques used, and mis-identification. The closeness of the two 1996 waterbird surveys in ordination space in relation to surveys of other wetlands (Fig 5) shows the waterbird survey methodology is robust when examining large changes in community composition, although sampling error may become important when looking at small changes. Similarly, mesh size and sector of the wetland sampled may affect results when small changes in invertebrate communities are being examined. Use of two or more pairs of invertebrate sweeps from different sectors and several waterbird surveys over a short time period each year (Lougheed *et al.* 1999) will reduce sampling error.

Salinity levels have not yet risen dramatically at Toolibin (Fig 2) and, therefore, the effects of increasing salinity on the fauna have been slight. Few waterbird species have stopped using the lake, which is not surprising given that most species found in fresh water in south-western Australia also occur in brackish and slightly saline water. The average long-term waterbird list for regularly filled fresh (< 3 000 mg L^{-1}) wetlands surveyed in the south-west between 1981 and 1985 was 18 species, for brackish wetlands (3 000-10 000 mg L^{-1}) it was 40 and for wetlands with spring salinities between 10 000 and 25 000 mg L^{-1} TDS it was 20 (Halse *et al.* 1993b).

Williams *et al.* (1991) proposed that freshwater invertebrates in low-land Australian rivers are salt-tolerant, based on sampling along the Blackwood River (downstream from Toolibin and Walbyring) in Western Australia and the Glenelg River in Victoria, neither of which showed a correlation between macroinvertebrate community composition and salinity. In contrast, Bunn & Davies (1992) argued that a suite of salt-sensitive species been lost from Western Australian rivers. Data from Toolibin and Walbyring appear to support Williams *et al.* (1991) and we suggest that most freshwater invertebrates of lentic wetlands in much of south-western Australia are comparatively salt-tolerant. Despite an approximate threefold increase in salinity, more invertebrate species were collected at both Toolibin and Walbyring in December 1996 than by Doupé & Horwitz (1995) in September 1992. Water mites (Acarina) were the only group collected by Doupé & Horwitz (1995) that were absent from the more saline 1996 samples.

Davis *et al.* (1993) recognized a group of freshwater invertebrates in wetlands around Perth with salinity tolerances up to 20 000 mg L^{-1}. Frey (1991, 1998) noted that seasonal flooding and drying of many wetlands in south-western Australia produced brackish conditions as the wetlands dried and, as a result, some chydorid cladocerans are adapted to moderate levels of salinity. *Pleuroxus* and related genera, in particular, appear to thrive in brackish water and are found in south-western Australia at salinities exceeding their observed ranges elsewhere. Halse (1981) collected the amphipod *Austrochiltonia subtenuis* and ostracod *Mytilocypris mytiloides* in the northern part of the Western Australia wheatbelt at higher salinities than they have been recorded in eastern Australia. It is only in the extreme south-west of Western Australia that a high proportion of the aquatic invertebrate fauna appears to be salt-sensitive (see Storey *et al.* 1993b; Edward *et al.* 1994; Horwitz 1997), although many of the species in granite rock pools of the wheatbelt may be restricted to fresh water (see species list in Bayly 1997) and salt-sensitive freshwater species do occur in other wheatbelt wetlands.

While our surveys suggest that salinization has caused only small changes in the Toolibin fauna to date, the occurrence of halophilous invertebrate species on the western side of the lake indicates that the lake may be approaching a salinity threshold, above which dramatic changes will occur. Other studies in Western Australia suggest the threshold is between 10 000 and 20 000 mg L^{-1} TDS (Halse *et al.* 1993b, Davis *et al.* 1993). Until biological responses to salinity are better documented, priority should be given to maintaining salinity of Toolibin below 10 000 mg L^{-1} TDS. The long-term management objective for the lake is that salinity should be less than 1000 mg L^{-1} TDS when it is full (Froend *et al.* 1997). This may allow salt-sensitive species that have disappeared from Toolibin, such as Australasian bitterns and purple swamphens, to use the lake again.

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Appendix

Aquatic invertebrate species collected in sectors of Toolibin and Walbyring Lakes on 18 December. x = present

	Toolibin East	Toolibin South	Toolibin West	Walbyring 1	Walbyring 2	Walbyring 3
MOLLUSCA						
GASTROPODA						
BASOMMATOPHORA						
Planorbidae						
Isidorella ? bradshawi Iredale				x	x	x
? Bayardella sp				x	x	x
ANNELIDA						
OLIGOCHAETA						
TUBIFICIDA						
Naididae						
Dero nivea Aiyer				x		x
Tubificidae						
Ainudrilus sp				x	x	x
OPISTOPHORA						
Opistophora sp				x	x	x
HIRUDINEA						
RHYNCHOBDELLIFORMES						
Glossiphoniidae						
Glossiphoniidae sp				x		
ARTHROPODA						
CRUSTACEA						
CLADOCERA						
Chydoridae						
Dunhevedia crassa King	x	x	x	x		
Leydigia aff. *australis* Sars				x	x	
Macrothricidae						
Macrothrix aff. *indistincta* Smirnov		x	x			x
Macrothrix aff. *capensis* (Sars)	x	x	x			
Daphnidae						
Daphnia cephalata King						x
Simocephalus vetulus Muller				x	x	x
OSTRACODA						
Cypridopsidae						
Sarscypridopsis aculeata (Costa)					x	
Cyprididae						
Alboa worooa De Deckker	x	x	x	x	x	x
Bennelongia australis (Brady)				x	x	x
Candocypris novaezelandiae (Baird)	x	x		x	x	x
Cypretta baylyi McKenzie				x	x	
Cyprinotus edwardi McKenzie	x	x	x	x	x	x
Diacypris spinosa De Deckker	x	x	x			
Mytilocypris ambiguosa De Deckker	x	x	x	x	x	x
Mytilocypris mytiloides (Brady)	x	x	x			x
Mytilocypris tasmanica chapmani McKenzie			x			
COPEPODA						
Centropagidae						
Boeckella triarticulata (Thompson)	x	x	x	x	x	x
Calamoecia ampulla (Searle)				x	x	x
Cyclopoidae						
Apocyclops dengizicus (Lepeschkin)	x	x	x			
Australocyclops australis (Sars)				x	x	x
Mesocyclops brooksi De Laurentiis *et al.*	x	x	x	x		x
Microcyclops sp				x	x	
AMPHIPODA						
Ceinidae						
Austrochiltonia subtenuis Hurley	x	x	x	x	x	x
INSECTA						
ZYGOPTERA						
Coenagriidae						
Xanthagrion erythroneurum Selys	x	x	x		x	x
Coenagriidae sp [1]		x		x		
Lestidae						
Austrolestes annulsosus (Selys)	x	x	x	x	x	x
ANISOPTERA						
Aeschnidae						

Appendix (continued)

	Toolibin East	Toolibin South	Toolibin West	Walbyring 1	Walbyring 2	Walbyring 3
Hemianax papuensis (Burmeister)	x	x	x		x	x
Gomphidae						
Hemicordulia tau Selys	x	x	x	x	x	x
Libellulidae						
Diplacodes bipunctata (Brauer)		x				
Orthetrum caledonicum (Brauer)		x				
HEMIPTERA						
Veliidae						
Microvelia sp				x		
Corixidae						
Agraptocorixa parvipunctata (Hale)	x			x	x	x
Micronecta robusta Hale	x		x	x	x	x
Sigara mullaka Lansbury		x		x		
Notonectidae						
Anisops gratus Hale				x	x	x
Anisops thienemanni Lundblad	x	x	x	x	x	x
DIPTERA						
Tipulidae						
Tipulidae sp	x	x				
Culicidae						
Anopheles annulipes s.l. Walker	x	x				
Chironomidae						
Chironomus occidentalis Skuse	x	x	x			
Chironomus oppositus Walker	x	x	x		x	x
Cladopelma curtivalva (Kieffer)	x	x	x			
Cricotopus albitarsus Walker					x	
Cryptochironomus griseidorsum Keiffer		x		x	x	x
Dicrotendipes conjunctus (Walker)	x	x	x	x	x	x
Kiefferulus intertinctus Skuse	x	x		x	x	
Polpedilum nubifer (Skuse)	x	x	x	x	x	x
Procladius paludicola Skuse	x	x	x	x	x	x
Tanytarsus fuscithorax Skuse	x	x	x	x	x	x
Ceratopogonidae						
Ceratopogoninae sp 1	x		x	x	x	x
Ceratopogoninae sp 2			x			
Ceratopogoninae sp 3						x
Forcipomyiinae sp	x				x	
Stratiomyidae						
Stratiomyidae sp 1	x					
Stratiomyidae sp 2	x	x	x		x	
Stratiomyidae sp 3		x				
Ephydridae						
Ephydridae sp 1			x			
Ephydridae sp 2	x	x	x			
LEPIDOPTERA						
Pyralidae						
Pyralidae sp	x	x	x			
TRICHOPTERA						
Ecnomidae						
Ecnomus sp					x	
Leptoceridae						
Notalina spira St Clair	x	x	x			x
Oecetis sp				x	x	
Triplectides australis Navas	x	x		x	x	x
COLEOPTERA						
Dytiscidae						
Allodessus bistrigatus (Clark)				x	x	x
Antiporus gilberti (Clark)				x	x	x
Lancetes lanceolatus (Clark)	x					
Liodessus inornatus (Sharp)	x					
Macroporus sp [2]					x	x
Megaporus howitti (Clark)					x	x
Necterosoma penicillatus (Clark)			x			
Rhantus suturalis (W S MacLeay)					x	

Table 3 (continued)

	Toolibin East	Toolibin South	Toolibin West	Walbyring 1	Walbyring 2	Walbyring 3
Sternopriscus multimaculatus (Clark)				x	x	x
Hydrophilidae						
Berosus discolor Blackburn [1,3]	x					
Berosus sp 1 [2]	x	x	x	x	x	x
Berosus sp 2 [2]	x	x	x	x	x	x
Enochrus elongatus (MacLeay)					x	
Enochrus eyrensis (Blackburn)				x		
Enochrus maculcieps (MacLeay)						x
Hydrophilidae sp [1,2]					x	x
Number of species	**41**	**41**	**36**	**44**	**51**	**46**

[1] Excluded from analyses; [2] coleopterans for which only larvae collected; [3] excluded from site and wetland total.

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Drainage evolution in the Moore-Monger System, Western Australia

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Abstract

The Moore-Monger Drainage System in the south-west of the Yilgarn Craton is examined in this study. It comprises the catchments of the Salt River rising near Mt Magnet and of the Monger River, both of which find their way into the Yarra Yarra Lakes. The Monger catchment includes both the extensive playas of Lake Monger and Lake Moore. All drainage lines are at low grade and extensively salinised with only intermittent flow. From the Yarra Yarra Lakes to the south there is an intermittent outlet along the line of the Darling Fault which unites with the north branch of the Moore River at Moora and further south with the east branch. These are short active rivers rising not far inland. The combined stream makes its way westwards to the coastal plain and the sea. Drainages located between the Moore-Monger System and the sea, such as the Hill, Arrowsmith, Irwin and Greenough Rivers, are also discussed. These rivers provide numerous examples of apparent disruption of drainage, diversion and reversal attributed to tectonic movements, in particular to upwarping of the cratonic margin in a belt some 70 km wide east of the Darling Fault and affecting the adjacent Perth Basin. This uplift appears gradually to die away towards the north and disappears at Morawa. An upward tilt to the north of the Western Shield has induced rivers to flow southward. This cannot be dated but the marginal uplift of the Yilgarn Craton is concluded to be late Eocene.

Keywords: watershed, drainage, river system, palaeodrainage

Introduction

This paper is a companion to a recent study of the South-West Drainage Division (Beard 1999). The Monger System was defined and included in that Division by Mulcahy & Bettenay (1972) but was omitted from Beard's recent paper on grounds of space. It was named from the large playa lake, Lake Monger, which is its central feature. As it includes the two branches of the Moore River which share the same drainage outlet, it is accordingly renamed the Moore-Monger System. It lies between the Avon System to the south and the Murchison System to the north, both of which include some active rivers, but the Moore-Monger System is less well-defined, consisting of flat country with drainage in the form of salt flats, indistinct channels and playas.

With the aid of recent geological and topographic maps the Moore-Monger System can be quite readily understood, but it contains some unusual and interesting features. The system (Fig 1) is roughly circular in plan with a diameter of about 300 km and an area of about 20 000 km^2. It is composite and contains several historically distinct elements, the unifying feature of which is that they converge into the Yarra Yarra Lakes in the west. The lakes have an outlet, now only intermittently active, leading southward through an incised valley to join the North Branch of the Moore River at Moora. To the south, beyond Gillingarra, the channel unites with the East Branch and the combined river turns to the west and reaches the sea across the coastal plain. Both branches of the Moore River are active during the winter and above Moora there is an active channel, the Coonderoo River, in the northern part of the valley from about 10 km south of Lake Pinjarrega.

The watersheds bounding the System and some internal ones are shown in Fig 1. Mulcahy & Bettenay (1972) united Lake Moore to the Avon System through a hypothetical Ninghan Palaeoriver rising in the Boodanoo Depression and running south along the line of Lake Moore, but it was later shown that Lake Moore in fact connects to Lake Monger (Beard 1973; Van de Graaf *et al.* 1977), A continuous watershed to the south of Lake Moore forms a ridge 100 m above the level of the lake and separates it from the Avon System.

The Moore-Monger System lies almost entirely on the Yilgarn Craton of the Western Shield, composed mainly of Archaean granite and gneiss with interdeveloped greenstone belts. The Darling Fault separates the craton from the Perth Basin to the west. The Fault is a major feature 1000 km long. It originated in the Palaeozoic to form the eastern side of a rift valley bordering the Yilgarn Craton. West of the fault a trough filled with sediments derived from adjacent continental landmasses. Movement along the fault ceased in the Neocomian (Playford *et al.* 1976), but sedimentation continued until the Late Cretaceous after which the Perth Basin and Yilgarn Craton were uplifted together. A narrow strip of the Perth Basin, part of the Dandaragan Plateau, is included in this drainage system.

The granite and gneiss terrain of the craton is generally of low relief sloping down gently from the central watershed at about 500 m to the Yarra Yarra Lakes at 240 m. Internal watersheds stand about 100 m above valley floors. The greenstone belts are generally hilly with the basalts forming large but isolated rounded hills as in the Gnow's Nest Range south-east of Yalgoo. Here they rise about 150 m above the surrounding country but are higher in the south as at Warriedar Hill (543 m) and Mt Singleton (678 m), a basaltic massif standing beside Lake

Moore. Except perhaps for Mt Singleton the greenstones do not appear to have influenced the general drainage pattern. The Salt River passes through the Gnow's Nest Range at Yalgoo as does Lake Monger at Warriedar, while the outlet from Lake Moore passes round the northern flank of Mt Singleton. Rocks exposed today in the Perth Basin consist mainly of Jurassic sandstones overlying Permian tillites. Some Cretaceous sandstones, greensand and chalk complete the sequence.

The general environmental features of this area including climate, geology and vegetation, have been described by Beard (1976, 1981). Rainfall averages 500 mm per annum in the south-west of the System, declining in the north-east to only 200 mm. Climate above the 300 mm isohyet has a winter rainfall maximum and is suitable for agriculture so that most original vegetation has been cleared. Further inland there is no assured growing season, the country is subject to pastoral use, and the vegetation has been modified to some extent but not cleared.

Methods

Methods followed were the same as for previous papers (Beard 1998, 1999). Fig 1 was produced by reduction from the latest maps in the National Topographic Map Series scale 1:250 000 (NATMAP, Canberra) and data from the previous papers were drawn upon, particularly for the definition of watersheds. Information on surface deposits was obtained from the local geological maps and memoirs published at 1:250 000 by the Geological Survey of Western Australia. For the interpretation of geological history, principal reliance was placed upon Playford *et al.* (1976) and Cockbain (1990). Relevant papers are referenced in the text and individuals consulted are listed in the Acknowledgments. The author has drawn upon his knowledge of the country acquired during field work for the Vegetation Survey of Western Australia.

Results

General description of the catchments

The Moore-Monger System consists of a number of discrete elements, several of which have been independent in the past. It is apparent that this has never been a single river catchment. It consists rather of separate catchments which have been amalgamated by tectonism into the single outlet of the Moore River (Fig 1). The northernmost component is the Salt River, rising near Mt Magnet, trending west to Yalgoo, then south to join the Monger River near Lake Nullewa. This was named the Yalgoo River by Mulcahy & Bettenay (1972) but appears as Salt River on official maps. The largest catchment is that of the Monger River, named by Mulcahy & Bettenay (1972.) from Lake Monger at its centre. Most of the catchment is very flat and drainage is marked by extensive playas. It comprises three main branches, a northen one of intermittent creeks coming down from Kirkalocka to Warriedar, a central one containing the extensive playa of Lake Moore, and a southern member consisting of the chain of salt lakes from Lake Hillman to Lake Goorly. The playas are surrounded by extensive salt flats with saltbush and samphire vegetation. These branches unite into the two-pronged lake system, called Lake Monger, consisting of long narrow playas over a distance of 60 km along each arm with little or no fall from one end to the other. The playas are continuous though often too narrow to be shown in width on the scale of Fig 1. Country along the chain of lakes from Lake Hillman to Lake Monger is even flatter and it would seem that little or no drainage ever passes today along this line. Drainage from Lake Monger to the west is blocked by a continuous north-south ridge averaging about 75 m in height above the lake bed, and an escape route exists round the north of this ridge in the vicinity of Perenjori, then north to Weelhamby Lake, west through Lake Nullewa connecting with the Salt River on the way, and thence south-west to the Yarra Yarra Lakes. As far as Lake Nullewa the alignment appears to be completely flat so that little drainage is likely to pass except in times of flood. From Lake Nullewa to the Yarra Yarra Lakes there is a drop of 35 m in 60 km, and there is a distinct channel winding between salt flats and pans. Exit to the west from the Yarra Yarra Lakes is again barred by a north-south ridge 75 m above the lake bed so that these lakes act largely as a sump. Two small creeks enter them from the east between Three Springs and Coorow. South of Coorow there is a more extensive system larger than the Moore River but mostly inactive. From its lower channel which normally feeds north into the Yarra Yarra Lakes, an overflow channel takes off for the south. It is probable that this takes some overflow in exceptionally wet years, but it is normally dry. There is no coherent channel, only a chain of salt lakes and salt flats such as Lake Pinjarrega. About 10 km south of the latter a channel takes shape, known as the Coonderoo River, fed by small streams rising in the Watheroo area. Still further south at the town of Moora this is joined by the Moore River from the east, an active stream, and the combined watercourse flows on due south for another 40 km until it joins the stream known as the Moore River East Branch, where it turns sharply to the west into a narrow valley issuing some 30 km further down onto the coastal plain. Across this it meanders to reach the sea at Guilderton. From the Yarra Yarra Lakes to the East Branch the drainage has taken a linear course heading slightly east of south, and it must be significant that this follows the line of the Darling Fault, mainly on its east side.

Salt River Catchment

The Salt River originates in salt flats south of the mining town of Mt Magnet. A coherent channel appears 50 km to the west and there are some small playas, but the channel is lost again approaching Yalgoo to the west. Past Yalgoo the Pindathuna Creek comes in from the north. It has a well-marked channel and is not salinised. West of the confluence the channel almost disappears for 10 km but is resumed again now flowing southwards past Mellenbye Station. This is shown in Fig 1 as a continuous river but is only a channel winding through salt flats and small playas. It meets the Monger drainage between Lakes Nullewa and Weelhamby.

The Salt River is cut off from the Greenough and Irwin Rivers to the west by a watershed branching off from the main east-west watershed and trending south-west and then south parallel with the Salt River. A similar continuous watershed can be traced dividing the Salt and Monger Rivers (Fig 1). Neither of these watersheds is topographically eminent, and map contours are needed to locate them. Headwater streams in the catchment are generally steep enough to be active *e.g.* the Pindathuna Creek above Yalgoo falls at 1.0 m km^{-1} but the main channel of the Salt River from a spot height of 369 m south of Mt Magnet down to Yalgoo at 312 m grades at 0.63 m km^{-1}, which is reduced to 0.25 m km^{-1} from Yalgoo to Lake Nullewa, steepening to 0.50 m km^{-1} from there to the Yarra Yarra Lakes. Grades on the main outlet of the system are: Yarra Yarra Lakes to Lake Pinjarra 0.16 m km^{-1}; Coonderoo River to Moora 0.47 m km^{-1}; Moora to confluence with East Branch 1.1 m km^{-1}.

Monger Catchment

The northern branch consists of intermittent small creeks between Kirkalocka and Warriedar, which are not salinised. The main channel drops at about 1.0 m km^{-1} over this distance. Downstream of Warriedar, the valley is occupied by the 60 km long north branch of Lake Monger which is almost flat, dropping at only 0.20 m km^{-1}. The middle branch of the catchment features Lake Moore, one of the largest playas in Western Australia, 120 km long and 10-20 km wide. A tributary, the Warne River, comes down from the north-east from the direction of Lake Boodanoo which is situated in a depression with no outlet. This is discussed below.

Spot heights on the bed of Lake Moore are between 301 and 304 m. There is an intermittently active outflow channel to Lake Monger which is about 20 m lower, passing round the north flank of Mt Singleton. It is possible that in the past the lake emptied through a parallel channel further south in addition. The third and southernmost branch of the catchment consists of a chain of playas and salt flats in very flat country leading NNE from Lake Hillman to the south branch of Lake Monger. A spot height of 297 m south-east of Lake Hillman gives a grade of 0.35 m km^{-1} along this stretch. From the south branch of Lake Monger, channels wind to the north-west past Perenjori and through Lake Weelhamby to Lake Nullewa. As Lake Nullewa is at the same elevation as Lake Monger it is evident that drainage can only pass along this stretch of 150 km in the event of exceptionally heavy rainfall.

Yarra Yarra Catchment

This term may be used to include drainages leading into the Yarra Yarra Lakes from the north-south ridge which obstructs flow from Lake Monger. They consist of shallow valleys floored with lacustrine deposits. The southernmost branch has become choked by an aeolian sandsheet that has been mapped and described by Beard (1979, 1984) and is shown in Fig 1. This was also mapped in the local geological survey (Carter & Lipple 1982) as "Qs, sand, mainly aeolian, quartz sand" without special comment. It is distinguished by its markedly yellow colour and a type of kwongan vegetation named the *Banksia-Xylomelum* alliance (Beard 1979). It was suggested by Beard (1984) that this sandsheet is a Quaternary deposit transported to the south-east from the Yarra Yarra Lakes area during an arid climatic phase with strong north-west winds. Several similar deposits elsewhere were attributed to this phase as well as the lunettes which typically border the south-east side of lakes in the southern part of the State.

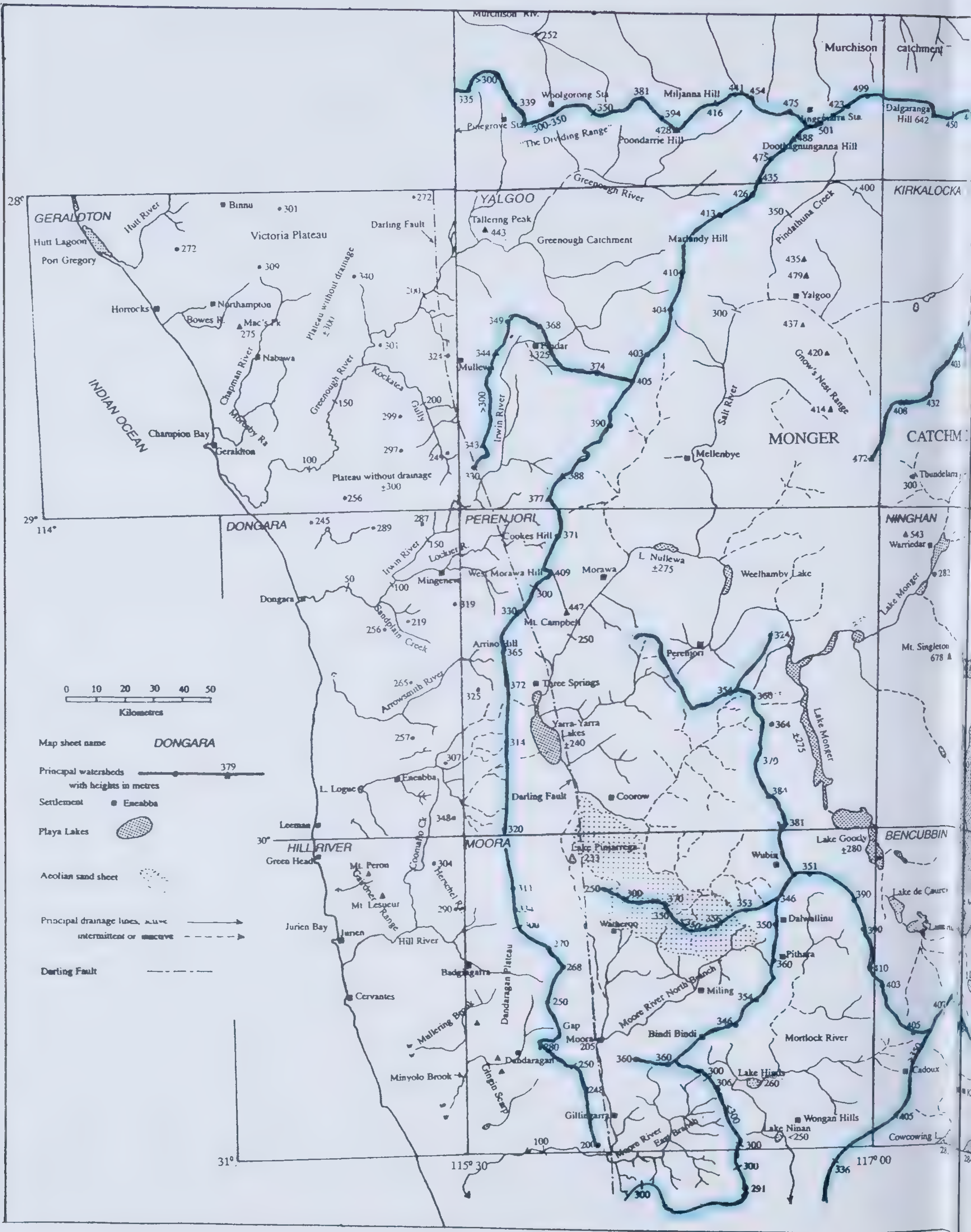
Moore Catchment

The Moore River on the Yilgarn Craton consists of two quite distinct streams, the so-called North Branch which flows down from the vicinity of Dalwallinu and Pithara to Moora, and the East Branch further south. Both of these rise in a continuation of the north-south ridge which obstructs the outflow of Lake Monger, and the same effect is visible. On the east side of the ridge there are west-flowing drainages aligned with those in both branches of the Moore River, but they have been ponded in Lake Hinds and Lake Ninan and deflected south to join the Mortlock River, part of the Swan-Avon System (Beard 1999). The two branches of the Moore River have been obstructed in turn beyond the Darling Fault by the higher ground of the Dandaragan Plateau. The East Branch has cut through to the coastal plain on the west, while the North Branch has developed a channel to join it following the Darling Fault southward and continuing the drainage line from the Yarra Yarra Lakes. The latter are at 240 m and Moora is at 205 m, a fall of 35 m in 100 km.

Coastal Catchments

Numerous catchments, some small and some large, have developed in the Perth Basin between the Darling Fault and the coast. North of the lower course of the Moore River there are several minor streams such as the Minyolo Brook and the Mullering Brook which rise on the Dandaragan Plateau, descend the escarpmemt and terminate in swamps on the coastal plain. The Quaternary Tamala Limestone, lithified from former dunes, mostly forms a barrier along the coast itself. The Hill River carries more water (or has done in the past) and has cut an outlet to the sea. A tributary, the Coomallo Brook, drains the country between the Gairdner and Herschel Ranges. This pattern is continued further north where some minor streams near Eneabba terminate in Lake Logue. The Arrowsmith River, which rises not far from the Yarra Yarra Lakes, turns north on the coastal plain and mostly evaporates in pans before entering a tunnel under the limestone. The Irwin River has cut an outlet to the sea through a substantial valley which broadens upstream in the Mingenew area into a belt of rolling country developed on erodible Permian sediments extending to the Darling Fault. The main Irwin River (not its tributaries) penetrates the Victoria Plateau further inland by a canyon-like feature, to rise near Pindar.

North of the Irwin River the Victoria Plateau forms a gently undulating plain with a general height of about 300 m. As the coastline trends away to the west, the plateau broadens until it is over 100 km wide. The coastal belt is dissected by the short Hutt and Bowes Rivers and the longer Chapman River. The Moresby Range which dominates Geraldton is a mesaform remnant of the plateau. The Greenough River winds across the whole plateau from north-east to south-west in incised meanders. Unlike the Irwin, the Greenough has had to dissect hard Jurassic sandstones and has not developed a broad valley nor significant tributaries. The sandy soil absorbs most of the precipitation so that extensive stretches of the plateau are without drainage. West of the


Murchison Riv.
Murchison
catchment
Woolgorong Sta
Pinegrove Sta
"The Dividing Range"
Miljanna Hill
Poondarrie Hill
Dalgaranga Hill 642
Doothagnunganna Hill
Greenough River
KIRKALOCKA
GERALDTON
Hutt River
Binnu
Hutt Lagoon
Port Gregory
Victoria Plateau
Darling Fault
YALGOO
Tallering Peak
Greenough Catchment
Macandy Hill
Pindathuna Creek
Yalgoo
Horrocks
Northampton
Bowes R.
Mac's Pk
Plateau without drainage ±300
Pindar
Mullewa
Nabawa
Chapman River
Greenough River
Kockatea Gully
Irwin River
Salt River
Gnow's Nest Range
INDIAN OCEAN
Champion Bay
Geraldton
Moresby Ra
MONGER
CATCHM
Mellenbye
Plateau without drainage ±300
Thundelarra
28°
29°
114°
DONGARA
PERENJORI
NINGHAN
Cookes Hill
Irwin River
Lockier R.
L. Nullewa ±275
Weelhamby Lake
Warriedar
Mingenew
West Morawa Hill
Morawa
Dongara
Sandplain Creek
Mt. Campbell
Lake Monger
Arrino Hill
Perenjori
Mt. Singleton 678
Three Springs
Arrowsmith River
Yarra-Yarra Lakes ±240
Lake Monger ±275
0 10 20 30 40 50
Kilometres
Map sheet name DONGARA
Principal watersheds with heights in metres 379
Settlement Eneabba
Playa Lakes
Aeolian sand sheet
Principal drainage lines, active
intermittent or inactive
Darling Fault
Eneabba
L. Logue
Darling Fault
Coorow
Leeman
Lake Goorly ±280
30°
HILL RIVER
MOORA
BENCUBBIN
Green Head
Mt. Peron
Coomallo Ck
Herschel R.
Lake Pinjarrega ±233
Wubin
Gairdner Range
Mt. Lesueur
Lake de Courcy
Watheroo
Dalwallinu
Jurien Bay
Jurien
Hill River
Pithara
Badgingarra
Dandaragan Plateau
Moore River North Branch
Miling
Cervantes
Mullering Brook
Gap
Moora
Bindi Bindi
Mortlock River
Dandaragan
Minyolo Brook
Gingin Scarp
Lake Hinds
Cadoux
Gillingarra
Wongan Hills
Moore River
East Branch
Lake Ninan <250
Cowcowing L.
31°
115° 30'
117° 00

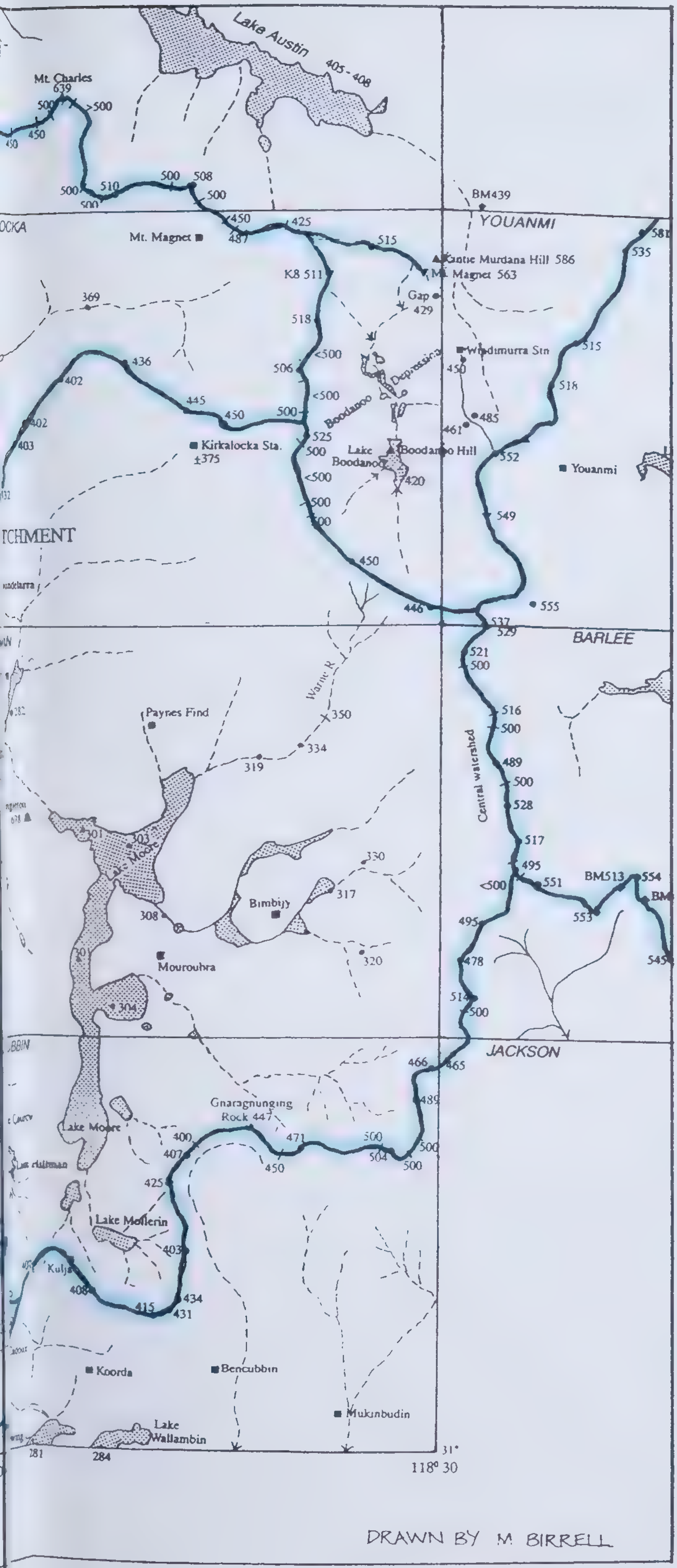


Figure 1. The Moore-Monger Drainage System and minor coastal catchments. Principal watersheds from Beard (1998).

Darling Fault there is a slight depression drained by the Kockatea Gully and small tributaries leading into the Greenough River, but there is otherwise no topographic break at the Fault. East of it the Greenough River drains a considerable catchment 120 km long and 100 km wide with numerous branches.

Boodanoo Depression

At the north-west corner of the Monger System is a feature which will be termed here the Boodanoo Depression. It is a valley trending north-south, 100 km long and 50 km wide which has no present outlet nor any obvious previous outlet, so that it is unclear whether it formerly drained south to Lake Moore or north to Lake Austin. The valley contains a 40 km long chain of playas. The largest at the southern end was named Lake Boodanoo in the geological survey (Baxter *et al.* 1983) after Boodanoo Hill, an outcrop of gabbro bordering the lake. There is also a Boodanoo Station a few kilometres further south. The lake has a spot height of 420 m. The topographic map shows minor watercourses leading into it from all sides. The depression is bounded on the east by the Central Watershed (Fig 1) at a height of about 550 m and a spur running north to Windimurra Station at 450 m. On the north the main ridge forming the watershed between the Monger and Murchison Systems, passing to the north of Mt Magnet town, continues to the east as far as Mt Magnet Hill (563 m), but its continuation south-east to join the Windimurra ridge descends to a col at 429 m. The western side of the Boodanoo Depression is bounded by a well-marked ridge at about 500 m which is in many places wide and capped by sandplains. However it does not extend round to the south of the depression to join the Central Watershed. Between Boodanoo and the tributaries of the Warne River there is no distinct ridge but a flat plain with spot heights of 450 and 446 m. It is therefore unclear whether the depression originally drained south or north. Beard (1973) favoured the south, Van de Graaf *et al.* (1977) the north. Current opinion seems in favour of the latter *e.g.* Commander (1989). If this is correct it is probable that the southward tilt of the Western Shield has been mainly instrumental in disrupting the drainage. Fig 1 excludes the depression from the Monger System.

Discussion

The drainage in the Moore-Monger System exhibits a number of peculiar features which need to be explained. Why is the westerly drainage of the Monger catchment obstructed by a north-south ridge which has apparently caused ponding and deposition of valley fill along the corresponding arm of Lake Monger? Why does this ridge continue southward separating the Mortlock and Moore Rivers? Why is the Salt River deflected southward at Yalgoo? At the edge of the Yilgarn Craton, why do these rivers not continue westward across the Dandaragan Plateau, developing instead a lengthy southward channel along the line of the Darling Fault? These anomalies resemble features of the other west coast rivers further south, *e.g.* the Avon, Murray and Collie systems, for which solutions were presented in a previous paper (Beard 1999) and can be applied here. A diagrammatic illustration (Fig 2, adapted to this area from Fig 5 of Beard 1999) shows successive stages of development in sections drawn across the System in an east-west direction from the Yarra Yarra Lakes to the Central Watershed at Youanmi. At the epoch of Stage 1, the formation of the Mesozoic surface of the Yilgarn Plateau is held to have been completed (Beard 1998), sloping gently down to the coast from the Central Watershed and drained by sluggish rivers in shallow valleys. The grades and levels were in accord with the high sea level of that time, with the shore line initially along the Darling Fault but gradually moved a few kilometres to the east of it by marine erosion. At this stage a height of 300 m for the Central Watershed has been assumed as it is in accord with later evidence.

At Stage 2, recession of sea level at the end of the Cretaceous has had the effect of raising the river mouths along the Darling Fault, discharging onto a plain below floored with the latest Upper Cretaceous deposits. This plain has become the Dandaragan and Victoria Plateaus. At the time, the surface was evidently not far above sea level. The Dandaragan Plateau area appears to have been exposed, but the Victoria was still receiving thin deposits into the Eocene. The assumption is made that the sea withdrew by an amount equal to the depth when the uppermost Cretaceous deposits were laid down, accepted as 200 m by Beard (1999) on advice from A E Cockbain (personal communication). The recession of sea level at this time, inferred from local geological evidence, is not necessarily in accord with global sea level changes (Haq *et al.* 1988) since local epeirogeny must also be considered. There is evidence for high sea level on the west coast of Western Australia during the Cretaceous, but none on the south coast, where transgression took place during the Eocene instead, leaving the west coast unaffected (summarised by Beard 1999).

Late Cretaceous regression having raised the river mouths above sea level, and rainfall being high at that epoch, it is likely that the rivers lowered their beds to the new base level, adjusting the valleys accordingly throughout the catchments. A period of 30 million years from the Maastrichtian to the Upper Eocene is available for this process. At Stage 3, post-Eocene, an uplift occurred in a belt 70 km wide east of the Darling Fault and for a certain distance west of it. The Dandaragan Plateau stands today at about 300 m above present sea level. Little erosion has taken place since uplift as the post-Neocomian deposits are relatively thin, the full sequence is present locally and there is no evidence for later deposits which have disappeared. However in uplift the surface was tilted up to the west so that the underlying Yarragadee Formation has become exposed along the crest of the Gingin scarp, continuing north into the Herschel Range. The Gingin scarp represents today the western edge of the uplift, the Perth Basin having subsided west of it into the Swan Syncline (Davidson 1995). This tilt of the plateau reversed drainage, causing ponding along the previous shore line which marine erosion had advanced for 2-4 km east of the actual line of the Darling Fault. A new outlet developed first south then west. In the same way the Victoria Plateau exhibits a drainage depression along the Darling Fault. The difficult and inefficient outlet from the Yarra Yarra Lakes has been to a large degree responsible for the lack of rejuvenation of the Salt and Monger Rivers, compared with the Avon and other rivers further south. At the present day the

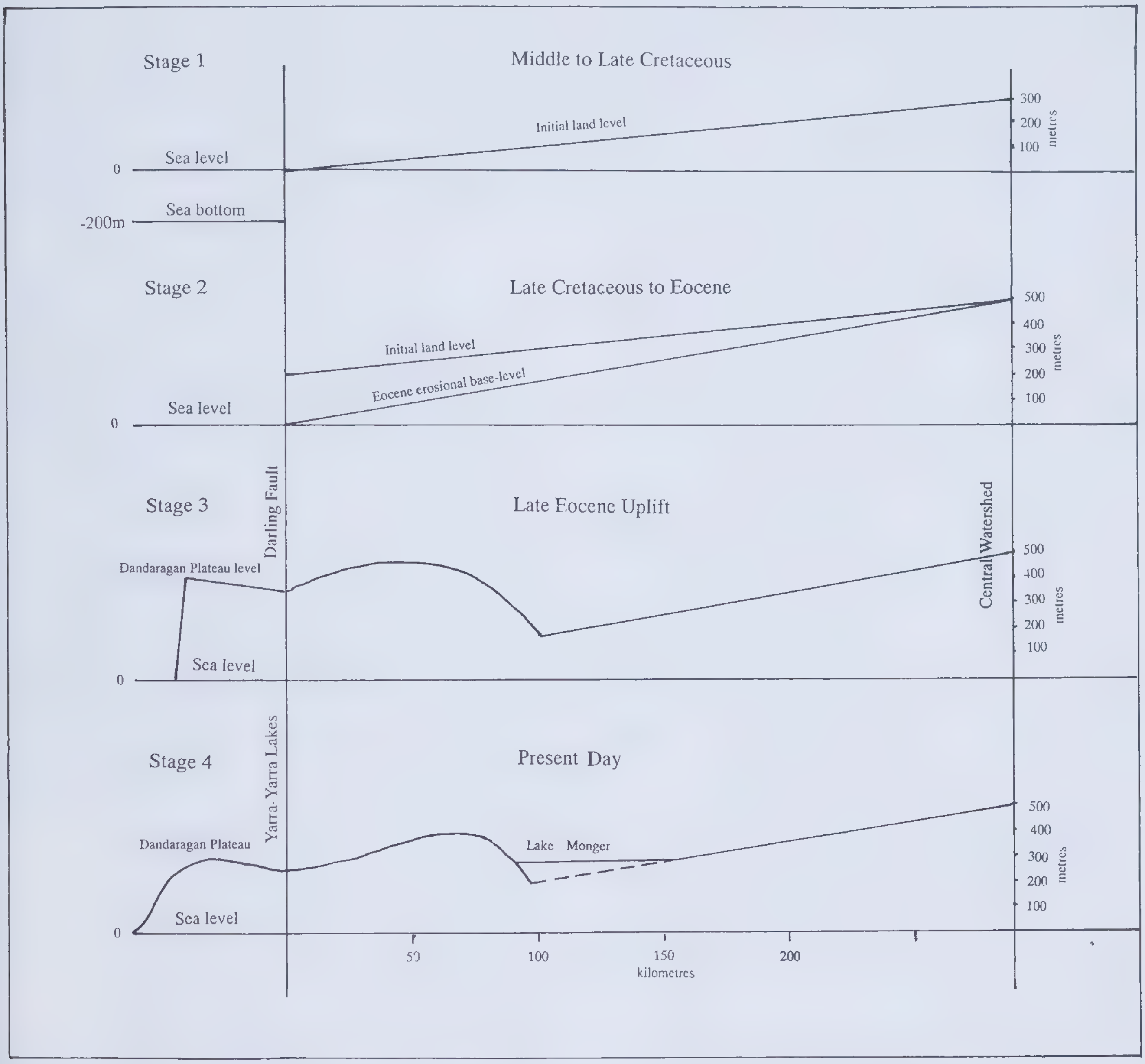


Figure 2. Cross-section of the Moore-Monger System drawn ENE from the Yarra Yarra Lakes to the Central Watershed at Youanmi, at successive geological stages.

Dandaragan Plateau narrows towards the south and gradually pinches out against the Yilgarn Plateau just north of the emergence of the Swan River from the Range. It is missing from the southern part of the Perth Basin until the corresponding feature of the Blackwood Plateau is reached. Its disappearance was formerly attributed to marine erosion (Playford *et al.* 1976) but is now seen as due to synclinal subsidence (Davidson 1995) which has carried down the Jurassic and Cretaceous sediments in the Perth Basin south and west of the present Gingin scarp, leaving the Dandaragan Plateau intact further north. No movement along the Darling Fault is implied, the syncline being treated as slumped against the edge of the Craton. It is this subsidence which has caused the rivers crossing the Darling Scarp to steepen their grades sharply in making a descent to the coastal plain (Beard 1999). This scope for rejuvenation was not available to the Salt and Monger Rivers terminating in the Yarra Yarra Lakes which today are at 240 m asl. The lakes must obviously contain some thickness (unknown) of sediments, but the basement must be at 150-200 m, allowing little fall from upstream.

It was concluded by Salama (1997) that uplift of the Darling Range obstructed flow of the Avon and Yilgarn Rivers which found a new outlet along the present course of the Avon through Northam. It can be seen (Fig 1) that this situation is repeated in the Monger System. A north-south ridge blocks the continued south-westerly flow of the Monger River, forming a lake 50 km long parallel to it, and backing the river up for 50 km upstream. Unlike the Avon the Monger River has been unable effectively to find a new outlet. Channels join it to the Salt River at Lake Nullewa but there is no fall from one end to the other. The System has remained at a much earlier stage of development. On the western slope of the uplift the decapitated rivers have established new catchments. It was shown in the previous paper (Beard 1999) that the two branches of the Moore River continue alignments that have been diverted to the south. North of them an unnamed river system between Coorow and Wubin probably preserves in its north branch the location of the original outlet of the Monger River.

At Stage 4 in Fig 2, *i.e.* the present day, there has been stability and erosion since uplift. The Dandaragan Plateau has developed a rounded contour, and the uplift east of the Darling Fault has been dissected and eroded down. The drainage channel through the Yarra Yarra Lakes was first excavated, then filled with sediment. Lake Monger formed at the back of the uplift. This model predicts that it should contain up to 75 m of sediment.

The marginal uplift in the Moore-Monger area seems to represent a declining northerly extension of a feature more strongly developed in the Darling Range further south. The country is hilly in the Moore River catchments, flattening towards the north. The uplift seems to die away before reaching Lake Nullewa. North of this there is still a slight rise traceable as the watershed between the Salt River and the Irwin and Greenough. This takes a north-easterly trend and in the form of a linear axis similar to the Jarrahwood Axis of Cope (1975). It is tempting to suggest that it may represent a minor axis of uplift which extended further to the north-east and was responsible for cutting off the upper Sandford River and so forming the huge playa of Lake Austin. On the other hand the southward deflection of the Salt River may have been only a response to the tilt of the Western Shield.

This tilt, demonstrated by Beard (1998), must be considered in addition to any other tectonic movements. The central watershed rises from 400 m in the south to a maximum of 750 m in the north so that the tilt is slight over a distance of 1036 km but has been inferred elsewhere to have influenced drainage patterns (Beard 1998, 1999). The Salt River west of Yalgoo abruptly turns to the south. After Lake Nullewa it is again south to the Yarra Yarra Lakes, then south again. The Dandaragan Plateau shows a slight tilt to the south, which is also visible in the south arm of Lake Monger, Lake Goorly and to the south of it, and on Lake Moore. Without being sufficient to reverse drainage, the tilting has caused ponding and promoted playa formation. After tilting, run-off water would have flowed to the southern part of Lake Moore and evaporated there instead of continuing to deepen the outflow channel at the north end. With the lower rainfall of the later Tertiary/Quaternary there would rarely be enough run-off to use the outflow channel so that salinity would increase and the lake gradually spread.

The formation of playas is an integral part of landscape evolution in semiarid areas. Small headwater streams still flow when there is rain and their silt is deposited to remain on the valley floor. Valleys gradually fill, and the fill would be uneven leading to ponding of runoff. Salinisation then sets in, the small lakes formed turn salt and become playas. Every time there is a flood, a layer of fine clay is deposited together with coarser material which may be blown out of the lake and deposited in dunes. The lake bed is slowly raised by this process and the playa spreads by absorbing adjacent country and killing the vegetation. Large playas are the ultimate stage. This process can be reversed at any time by the return of more pluvial conditions or reinitiated. Conversion of a valley from attrition to accumulation may also be effected by epeirogenic movement. Sinking of a valley may convert it to internal drainage while crustal uplift or tilting may do the same or cause either reduction of reversal of flow. All these effects are observable in Western Australia.

Conclusions

The most important conclusion from this paper is that it provides additional evidence for marginal uplift along the western side of the Yilgarn Craton from Morawa down to the south coast, a distance of some 600 km. The width of the uplift zone is about 70 km. No evidence exists as to whether it was raised by faulting or marginal upwarp. North of it there is evidence for a possible minor uplift axis trending to the north-east above Morawa and perhaps extending into the Murchison River catchment west of Lake Austin.

No date can be suggested for the north-south tilt of the Western Shield, but the uplift of the western margin of the craton probably took place in the late Eocene (Beard 1999). A reconstructed palaeodrainage is given for the Eocene period after recession of Cretaceous high sea level but preceding the late Eocene uplift. The geological maps are most helpful in establishing former courses as they show how valley deposits extend close to one another on either side of present watersheds. Continuing more or less west from Yalgoo the Salt River probably connected with a branch of the Greenough River. On reaching the Darling Fault the valleys of the Greenough and its tributaries change their form. They unite into a single stream which has incised earlier meanders into the plateau, showing that it perpetuates a course established when flowing out across the sedimentary plain at the close of the Cretaceous. The valley of the Irwin River below Mingenew is straighter, deeper and wider than that of the Greenough so that it is tempting to infer that it must have received substantial run-off from the Yilgarn Craton. Connections may have occurred through its tributary the Lockier. Drainages rising in the Gnow's Nest Range may have continued west at Mellenbye to connect with the next valley (now dry), following it down to a side valley which comes in with an anomalous direction heading to the north-east, and through this to the Lockler River north of Cookes Hill. The development of the Irwin west of the Darling Fault has also been strongly influenced by its exploitation of easily erodible Permian sediments.

The next connection further south is with the Arrowsmith River where there are clear signs of a link to interior drainage at Arrino. At both the north and south ends of the Yarra Yarra Lakes there are signs of possible westerly flow. The upper catchment of the Coonderoo River at Watheroo seems to have connected to the Hill River while the Moore River North Branch shows clear signs of having flowed west to the Minyolo Brook. A valley containing salt flats and small playas, *e.g.* Lake Dalaroo, extends due west from Moora beyond which it is only another 4 km to the source of the Minyolo. The col in between appears to be about 60 m above the Moore River at Moora.

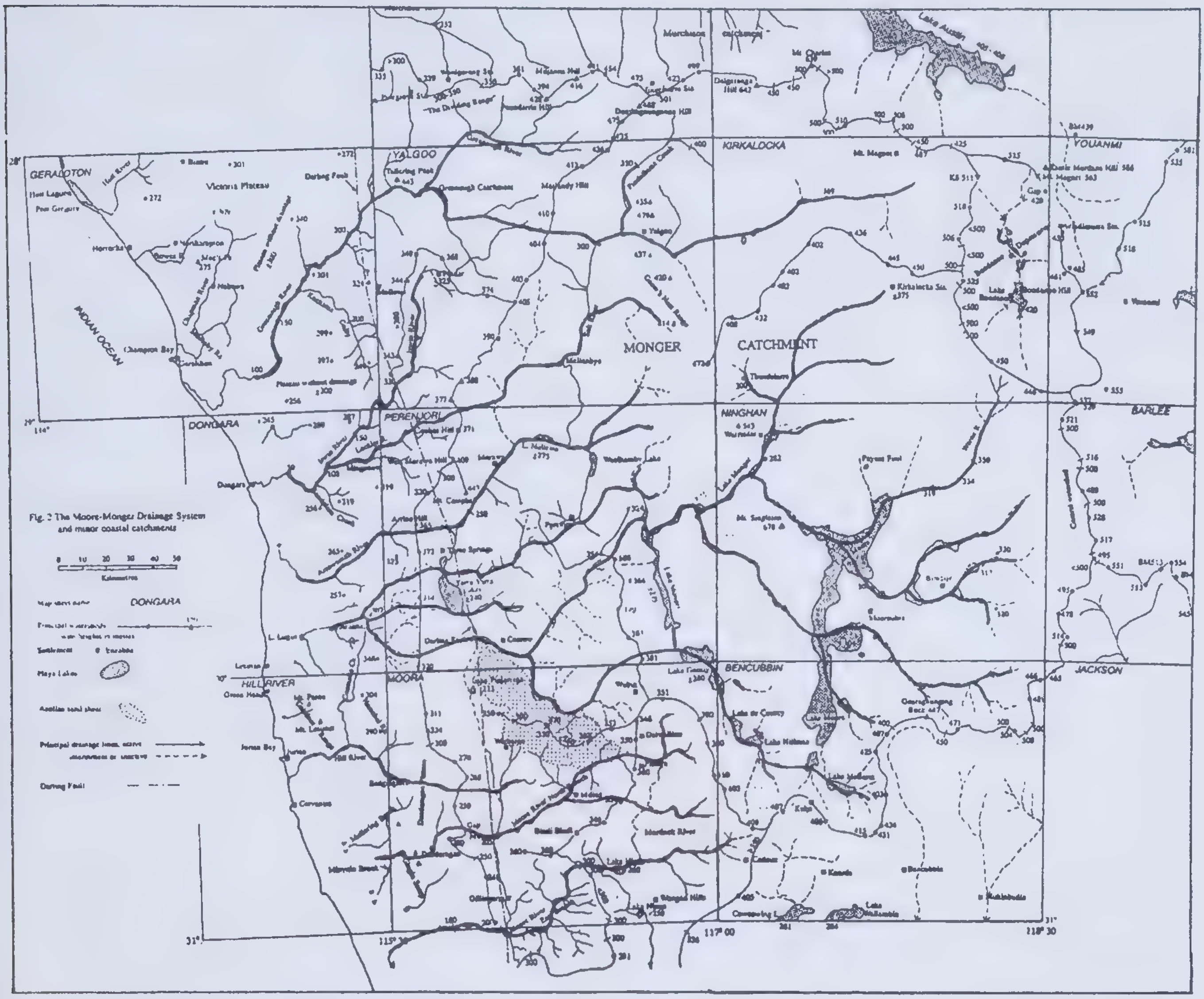


Figure 3. The Moore-Monger area showing inferred drainage patterns of the early Tertiary superposed on Fig 1. Position of the Eocene shoreline is not known.

Further inland it seems clear that drainages must have crossed the present watershed which has resulted from the uplift. The geological map shows that deposits in valleys leading to the Yarra Yarra Lakes are almost continuous with others leading the other way into Lake Monger in the vicinty of Perenjori, with only a short interruption at the watershed. This applies also at several places further south. One valley which leads into the north end of Lake Monger from a point on the watershed marked 366 (Fig 1) was studied by Salama *et al.* (1993) who reported that the watercourse in the 23km long catchment is underlain by alluvial sediments to a depth of 28m. These are undated and were presumably deposited after drainage reversal. The main channel from the Monger catchment may have used this valley or another slightly further south. Northernmost drainages into Lake Moore are shown in Fig 3 as using the present outlet, and the southern as using the alternative outlet south of Mt. Singleton.

For the headwaters of the Mortlock River the geological map (Baxter & Lipple 1985) suggests a former course to the west north of Pithara as well as a possible connection due east of Dalwallinu from Lake Goorly to Lake Hillman, as it seems reasonable to suggest that the north-trending section here of the main watershed between the Moore-Monger and Avon Systems may be an artifact of the uplift. This watershed would originally have taken a south-westerly trend through Cadoux. Other branches of the Mortlock River are in line for connections to the Moore River. From Lake Hinds the geological map suggests a former course to the west via a gap in the ridge at Gabalong 10 km south of Bindi Bindi. It does not seem possible to throw more light on the situation unless drilling data become available.

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Notes on ....

Cocoon formation and metabolic depression by the aestivating hylid frogs *Cyclorana australis* and *Cyclorana cultripes* (Amphibia: Hylidae)

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Abstract. Two northern Australian burrowing hylid frogs, *Cyclorana australis* and *C. cultripes*, form a cocoon when induced to aestivate. The cocoon completely encases the frog except for the external nares and it consists of shed multiple layers of outer epidermal cells interspersed with ground substance. The cocoon of *C. australis* was about 24 μ thick and had about 34 layers (formed at about 0.7 layers day^{-1}), and the cocoon of *C. cultripes* was about 16 μ thick with about 51 layers (about 0.6 layers day^{-1}). Evaporative water loss decreased from 15.8 to 1.1 mg g^{-1} h^{-1} for cocooned *C. australis*, and 15.1 to 1.3 mg g^{-1} h^{-1} for cocooned *C. cultripes*; these correspond to cutaneous resistances of 3 to 112 sec cm^{-1} for *C. australis*, and 0 to 223 sec cm^{-1} for *C. cultripes*. Metabolic rate declined significantly with aestivation by 70% from 0.160 to 0.049 mg O_2 g^{-1} h^{-1} for *C. cultripes* after about 6 weeks of cocoon formation, and respiratory exchange ratio decreased significantly from 0.98 to 0.68. Metabolic rate declined insignificantly by 40% from 0.158 to 0.095 ml O_2 g^{-1} h^{-1} for aestivating *C. australis*, which remained more responsive during aestivation than *C. cultripes*. All species of *Cyclorana* so far investigated aestivate and form a cocoon of similar structure and efficiacy, but the most tropical species *C. australis* does not appear to as effectively depress metabolism as other species.

Key words: hylid frog, *Cyclorana*, aestivation, cocoon, evaporative water loss, metabolic depression

Introduction

Frogs that inhabit the arid areas of Australia often have anatomical, physiological and behavioural strategies to enhance their survival over extended dry periods. For example, the burrowing frogs so far investigated (the hylids *Cyclorana platycephala*, *C. maini* and *Litoria alboguttata*; and the myobatrachids *Neobatrachus* spp) aestivate during dry conditions. They form a cocoon of multiple layers of shed epidermal cells, which is an effective barrier to evaporative water loss, and depress their metabolic rate to about 25% of resting to conserving energy reserves (Lee & Mercer, 1967; van Beurden, 1984; Withers, 1993, 1995, 1998; Withers & Richards, 1996; Christian & Parry, 1997).

This study continues these previous investigations of cocoon formation and metabolic depression during aestivation, and examines cocoon formation, evaporative water loss and metabolism for two hylid species, the tropical-zone *C. australis* and the central-northern *C. cultripes*.

Materials and Methods

Specimens of *C. australis* and *C. cultripes* were collected near Kununurra, Western Australia, after heavy rain in January 2000. The frogs were air-freighted to Perth, washed in tap water, and placed individually in plastic chambers with a small hole in the lid for ventilation. The chambers were placed in a dark cupboard and the frogs left undisturbed except for inspection every 2 to 4 days. Ambient temperature was 24 ± 1 °C.

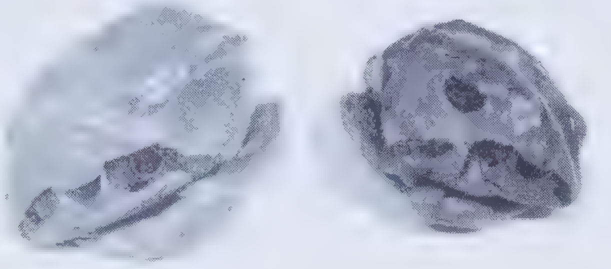

Figure 1. Aestivating *C. australis* (left) and *C. cultripes* (right), showing semi-transparent cocoon enveloping the entire body, except for the nares.

After 2 days to acclimate the frogs to the laboratory conditions, resting metabolic rate and evaporative water loss were determined by flow-through respirometry. The frog was placed in a cylindrical glass chamber, on a plastic mesh grid to expose the ventral as well as dorsal skin to a flowing airstream (100-400 ml min^{-1}). Excurrent oxygen, carbon dioxide and water contents were measured with a Servomex paramagnetic O_2 analyser, a Qubit infra-red CO_2 analyser, and a Vaisala thin-film capacitance humidity meter (see Thompson & Withers, 1998). After a further 46 to 50 days, aestivating frogs were re-examined, then their cocoon removed for examination using a Phillips 505 scanning electron microscope. Both air-dried and formol saline-preserved pieces of cocoon were examined, to measure thickness and to count the number of cocoon layers (see Withers 1995).

Results

Both species became quiescent, assumed the water-conserving posture, and formed a cocoon (Fig 1). *C. australis* remained more responsive to handling than *C. cultripes*, and would more often move their eyes and limbs when disturbed than *C. cultripes*.

The cocoon of both species formed a semi-transparent, shiny film, closely adherent to the skin over the entire body surface

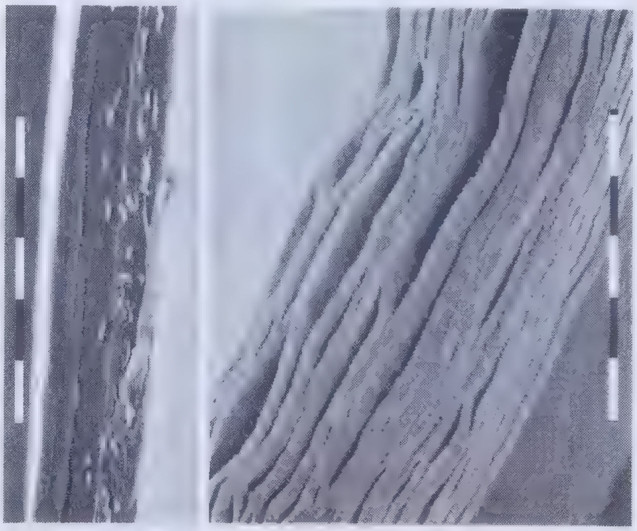

Figure 2. Scanning electron micrographs of cocoon showing the normally compacted structure (left; air-dried specimen, *C. cultripes*) and the layered structure that is more obvious after the cocoon is soaked in formol saline (right; formol saline fixed, *C. australis*). Scale bars are 10 μ.

Table 1. Number of days for cocoon formation, number of cocoon layers, cocoon thickness (μ), layers formed per day, thickness per layer, resistance per layer, and resistance per thickness (see Table 2 for resistance) for two individuals of both *C. australis* and *C. cultripes*.

	C. australis	*C. cultripes*
days	46	51
layers	34	32, 33
μ	23.1, 24.5	16.7, 14
layers d^{-1}	0.74, 0.74	0.65, 0.63
μ $layer^{-1}$	0.68, 0.72	0.51, 0.44
R $layer^{-1}$	3.3, 3.3	6.8, 7.0
sec cm^{-2}	4.6-4.9 10^4	13.4-15.9 10^4

except for the external nares through which the frogs continued to breathe. It was sealed over the eyes, mouth and cloaca. The cocoon consisted of multiple thin layers of shed epidermis (Fig 2). *C. australis* shed 34 layers of skin in 46 days, with a mean thickness of 0.7, compared with *C. cultripes* that formed 32.5 layers in 51 days with a mean thickness of 0.48 μ per layer. (Table 1).

Evaporative water loss declined significantly for both species during aestivation, with an increase in resistance from about 1 to 223 for *C. cultripes* and 112 for *C. australis* (Table 2). The resistance per layer, and resistance per unit thickness, was lower for the cocoon of *C. australis* than *C. cultripes* (Table 1).

The resting metabolic rate (RMR) of *C. cultripes* declined significantly by 70% during aestivation to about 30% of RMR. The metabolic rate of *C. australis* declined, but not significantly, to about 60% of RMR (Table 2). The carbon dioxide production declined similarly. For *C. cultripes*, the respiratory exchange ratio declined significantly from 0.98 for awake frogs to 0.68 for aestivating frogs, but RER was extremely variable and did not alter significantly for *C. australis*.

Discussion

This study indicates that two further species of *Cyclorana* aestivate and form a cocoon, similar to the more arid *C. maini* and *C. platycephala*, and sub-humid to tropical *C. novaehollandiae* (Withers 1995, 1998). Cocoon structure is similar for the five species of *Cyclorana* investigated, with cocoon layers (about 0.2-0.7 μ thick) added to the cocoon at a rate of about 0.6-1.1 layers per day, conferring a resistance of about 3-10 sec cm^{-1} per layer. It is of interest to determine whether the further seven species of *Cyclorana* that have yet to be studied (*brevipes, cryptotis, longipes, maculosa, manya, vagita, verrucosa*; Cogger 1992), will also aestivate and form a similar cocoon.

The extent of metabolic depression by *C. cultripes* is similar to that of other aestivating *Cyclorana* spp, and also various *Neobatrachus* spp. Withers (1993) reports depressed metabolic rate (DMR) as 8 – 33% of RMR for six *Neobatrachus* spp and two *Cyclorana* spp. In contrast, metabolic depression was to only 60% of RMR for *C. australis*, which remained more responsive during aestivation than *C. cultripes* and other *Cyclorana* spp previously examined. Perhaps energy conservation from metabolic depression is not as important for this larger frog that inhabits wet tropics, as its higher body mass confers an energy consumption advantage (lower mass-specific metabolic rate) and rainfall in the monsoonal tropics is more predictable than in the arid areas where irregular rainfall might require burrowing frogs to aestivate for one or more years and necessitate metabolic adaptive strategies to survive these long periods without feeding. Whether metabolic depression during aestivation will be similarly less pronounced for other tropical *Cyclorana* species (*brevipes, cryptotis, longipes, maculosa, manya, vagita*; Cogger 1992) remains to be determined.

Table 2. Body mass, oxygen consumption rate ($\dot{V}O_2$; ml g^{-1} h^{-1}), carbon dioxide production rate ($\dot{V}CO_2$; ml g^{-1} h^{-1}), respiratory exchange ratio (RER = $\dot{V}CO_2/\dot{V}O_2$), evaporative water loss (EWL; mg g^{-1} h^{-1}) and resistance to water loss (R; sec cm^{-1}). Values are mean ± standard error, with sample size (n). P is probability of difference between awake and aestivating values (t-test).

C. cultripes	Awake (*n=10*)	Aestivating (*n=6*)	P
Mass	11.7±1.0	9.8±1.2	
$\dot{V}O_2$	0.160±0.021	0.049±0.007	0.001
$\dot{V}CO_2$	0.145±0.011	0.033±0.006	<0.001
RER	0.98±0.086	0.68±0.09	0.024
EWL	15.1±1.7	1.30±0.17	<0.001
R	-0.9±0.7	223±30	0.001
C. australis	Awake (*n=8*)	Aestivating (*n=12*)	
Mass	44.2±9.4	32.1±5.4	
$\dot{V}O_2$	0.158±0.037	0.095±0.011	>0.05
$\dot{V}CO_2$	0.100±0.030	0.082±0.014	>0.05
RER	0.67±0.11	0.96±0.20	>0.05
EWL	15.8±2.1	1.1±0.1	<0.001
R	2.7±0.1	112±12	<0.001

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Note from the Hon Editor:

This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). References are abstracted from Current Contents, Biological Abstracts and Sci Finder Scholar by searching for Western Australia in the title and abstract.

P C Withers,
Honorary Editor,
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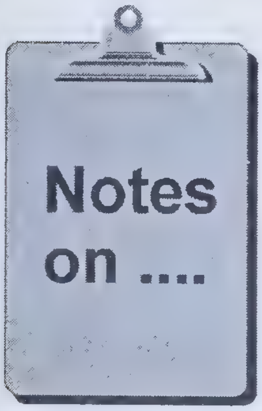
Journal of the Royal Society of Western Australia, 83:59, 2000



Note from the Honorary Editor:
"Notes on ...."

The Society wishes to encourage scientists to publish short notes dealing with original research done in any branch of the natural or physical sciences in Western Australia, or concerning some aspect of natural or physical science of relevance to Western Australian scientists. Notes will be restricted to a maximum length of two printed pages. Manuscripts submitted as a Note will be reviewed in the same manner as full articles, but I hope that referees will be willing to provide reviews within 7 days and so the review process should be quite rapid.

Our objective in publishing "Notes on ..." is to encourage the dissemination of research findings that might not be enough for a full paper but nevertheless be of interest to other scientists, especially those in Western Australia. In addition, specific aspects of student theses, particular findings of commissioned reports, or isolated observations of significance might be well presented as a one or two page note.

The note in this issue by Withers & Thompson illustrates the format for "Notes on ..." This note, for example, consisted of 1700 words, in addition to two single column figures and two single column tables. Authors should ensure optimum size and use of tables and figures, and keep text to a minimum, to ensure that notes can be formatted to fit a maximum of two printed pages. If necessary, editorial changes will be made to ensure that notes do not exceed two printed pages. To assist authors in preparing notes, a template document (Microsoft® Word and rtf files) is available on the RSWA web site (see JRSWA page).

I hope that members will take this opportunity for rapid publication of short Notes.

Philip Withers
Honorary Editor
Journal of the Royal Society of Western Australia

Journal of the Royal Society of Western Australia, 83:61, 2000

Obituary: Norman H. Brittan

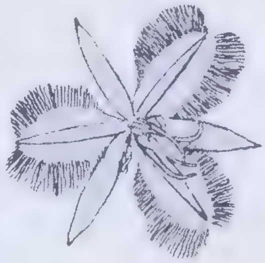
(7 September, 1920 – 19 April, 2000)

A former President of the Royal Society of Western Australia, Norman Brittan passed away on 19 April, 2000.

Born on 7 September 1920 at Whitley Bay, Northumberland, Norman attended Rutherford College (Newcastle, UK) and went on to complete his BSc (1st class Honours) in Botany from the University of Durham in June 1941. His tertiary education was interrupted at this point by the war, in which he served as an army officer in Radar with REME. Returning to his studies after the war, he was awarded his PhD in 1950 from the University of Durham (King's College).

In September 1950, Norman migrated to Perth where he took up a position as lecturer in the Botany Department at the University of Western Australia (where he spent his whole professional career). His main areas of interest were plant anatomy, physiology and genetics, linked to systematics, and he taught in all these areas as well as supervising the research of several graduates in the Faculties of Science and Agriculture. Early in his time here he studied the legume genus *Kennedia*, producing a systematic and ecological overview with J H Silsbury in 1955. He then turned to the monocots, and the genus *Thysanotus* (fringed lilies) in particular. His research over the following decades (including periods at the Royal Botanic Gardens, Kew, where he developed expertise in electron microscopy) resulted in a number of papers, with the description of 25 new species of *Thysanotus*. It was a great joy for Norman to explore outback regions for specimens of his speciality genus *Thysanotus*. His work culminated in a revision of the genus in 1981 and an account for the 'Flora of Australia', published in 1987. A distinctive new species closely allied to *Thysanotus* was placed in a new genus, *Murchisonia* (1971), and another species was added in 1986. He also wrote *Arthropodium* and *Dichopogon* for the 'Flora'. Norman competently prepared his own line drawings. Following his retirement at the end of 1985 he was made an Honorary Research Fellow in the Department of Botany, during which period he completed his 'Flora of Australia' work.

He was a long-standing member of the Royal Society Council (1953–63) serving variously as Council Member, Secretary, Vice-President and as President in 1960–61. At the end of his term he gave a Presidential Address entitled 'Variation, Classification and Evolution in Flowering Plants—with particular reference to *Thysanotus*' (*Journal of the Royal Society of Western Australia* 45:1–11, 1962).



Thysanotus pseudojunceus from Brittan (1960)

Norman was associated for many years with the University's arm of the Student Christian Movement. He was an avid listener to classical music of many composers, both recorded and at concerts. Gentle and somewhat retiring, he was ever ready to advise and assist students and colleagues. He had a quite formidable talent at resolving complex issues, which made him an obvious choice on the University's timetabling committee, and in advising students as the Sub-Dean of the Faculty of Science (1962/63).

He is commemorated in the specific epithet of *Lomandra brittanii* Choo, named in 1984 by one of his post-graduate students.

Alex George and Bill Loneragan

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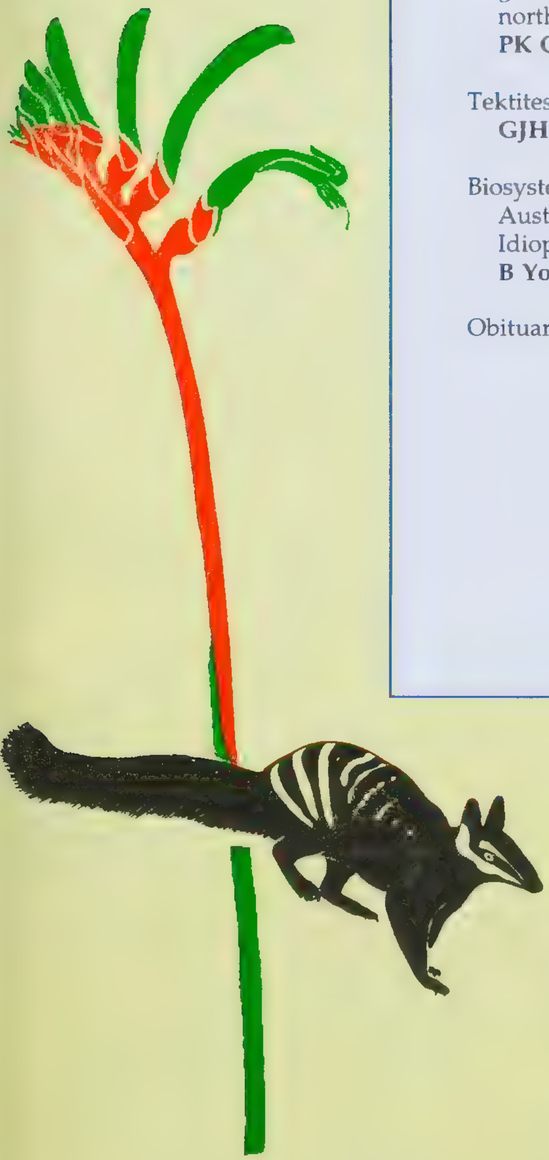

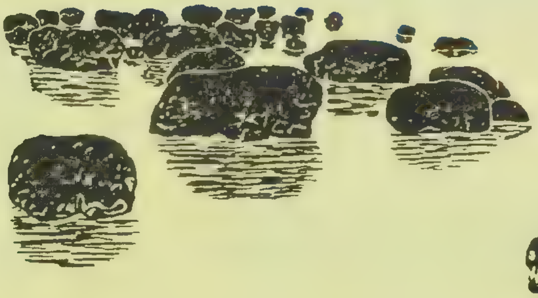

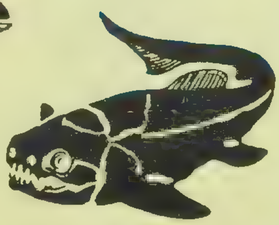

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Regeneration of degraded woodland remnants after relief from livestock grazing

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Abstract

Clearing for agriculture has left a mosaic of remnants of native vegetation in a matrix of agricultural land. Protection of these remnants is an important issue in minimising the effects of land degradation and for nature conservation in agricultural areas of Western Australia The first approach to restoration is to remove the disturbing element, and in the case of livestock grazing this requires fencing to exclude stock and allow natural regeneration of the remaining vegetation. The description of this natural regeneration process is an essential first step in developing restoration techniques and management strategies for areas of degraded native vegetation. This article describes the changes in the vegetation for three different vegetation types in degraded woodland remnants in south-west Western Australia after livestock grazing has been excluded for seven years. These include vegetation types characterised by the overstorey species including jarrah (*Eucalyptus marginata*) marri (*Corymbia calophylla*), wandoo (*Eucalyptus wandoo*) and sheoak (*Allocasuarina fraseriana*). Species of the families Poaceae and Asteraceae were dominant in the understorey in grazed remnants for all vegetation types, with the majority of these species being exotics. After seven years, floristic similarity between fenced and grazed plots had decreased while similarity between fenced and ungrazed had increased, in all vegetation types. Native vegetation in jarrah sites have shown the greatest response to cessation of livestock grazing with an increase in species richness and diversity while wandoo and sheoak plots have showed little change. In terms of plant life forms, there was a significant increase in number and cover of native perennial grasses, perennial herbs and shrubs in the fenced jarrah plots. Response of annual species have tended to fluctuate with annual fluctuations in rainfall. There was variation in response to livestock grazing of different vegetation types within these woodland remnants. At a relatively early stage of decline in a remnant, the structure and composition of the native community can be re-established by excluding stock. However, under severe and prolonged grazing, regeneration will be more difficult. These results indicate that the degree of difficulty of restoration will vary for different community types even within the broad category of jarrah and wandoo woodlands. Therefore, when managing for the restoration of remnants of native vegetation, consideration of vegetation type is an important factor.

Introduction

Widespread clearing for agriculture has left a mosaic of remnants of native vegetation in a matrix of agricultural land. Protection of these remnants is an important issue in minimising the effects of land degradation and for nature conservation in agricultural areas of Western Australia (Saunders *et al.* 1987; McFarlane & George 1992; Hobbs & Saunders 1993) and throughout Australia (Landsberg & Wylie 1991; Lamb 1994). The majority of these remnants have been subjected to varying levels of disturbance, including livestock grazing, which compromises their ability to be self-regenerating (Saunders *et al.* 1991) and therefore they are in various stages of degradation. The first approach to restoration is to remove the disturbing element (Lamb 1994) and in the case of livestock grazing this requires fencing to exclude stock and allow natural regeneration of the remaining vegetation. The description of this natural regeneration process is an essential first step in developing restoration techniques and management strategies for areas of degraded native vegetation. Livestock grazing exclusion experiments have been conducted in many different vegetation types in Australia, such as alpine grasslands and heathlands in eastern Australia (Wimbush & Costin 1979; Wahren *et al.* 1994), chenopod shrublands in the semi-arid zone (Graetz & Tongway 1986), temperate shrub-dominated woodlands (Hobbs 1989; Pettit *et al.* 1995) and grassy woodlands (Gibson & Kirkpatrick 1989). These studies indicate that differences in vegetation response to relief from grazing pressure are related to intensity of grazing, history of grazing and vegetation type (Milchunas & Lauenroth 1993) and often the results are not assured (Yates & Hobbs 1997).

Response of individual plant species to grazing varies according to growth form and reproductive strategy. For example, annual species are more tolerant of disturbance, due to their fast growth rates and early and prolific seed set, than perennial species which tend to be comparatively slow growing and usually require several years to reach reproductive maturity (Grime 1974). Other groups such as geophytes can avoid heavy grazing pressure by having above-ground growth occurring in winter and spring, and dying back to an underground storage organ over summer (Pate & Dixon 1981) when grazing pressures are usually heaviest. It may also be useful in ecological terms to suggest the regenerative capacity of a plant community according to species functional groups (Hobbs 1992) is based on life forms or reproductive strategies (Armstrong 1993). Maintenance of one or more species representative of each functional group may be an important strategy in restoration/ management of degraded remnants (Hobbs 1992).

In south-west Western Australia, jarrah (*Eucalyptus marginata*) woodland comprises many different plant communities distinguished by the structure and composition of the understorey (Havel 1975). These differences are usually related to soil type and moisture regime (Bell & Heddle 1989). Whether these different plant communities demonstrate the same response to degradation by livestock grazing and capacity for recovery after the exclusion of stock is unknown. Differences in response have important implications for the management for restoration of these remnants.

Pettit *et al.* (1995) examined the floristics of a large number of jarrah woodland remnants subjected to varying levels of livestock disturbance. This paper reports on the natural regeneration of three different vegetation types in degraded jarrah woodland remnants in south-west Western Australia after livestock grazing has been excluded for seven years. These include vegetation types characterised by the overstorey species jarrah (*E. marginata*); marri (*Corymbia calophylla*); wandoo (*Eucalyptus wandoo*) and sheoak (*Allocasuarina fraseriana*).

Methods

Study sites were located within remnants of native vegetation near the town of Darkan in the south-west of Western Australia (33° 30' S, 116° 30' E) where approximately 67% of the native forest has been cleared for farmland (Loh *et al.* 1989). The landscape and soils of these sites are typical of the Beraking Valley form, with slopes dominated by gravely sandy soils with some ferruginous duricrust on the hilltops (Mulcahy & Bettenay 1972). The sites are at the eastern extent of the northern jarrah forest where jarrah and to a lesser extent marri and wandoo form a woodland or open forest (Dell & Havel 1989). There is a mid-storey of small trees such as *A. fraseriana*, *Banksia grandis* and *Persoonia longifolia*, and the understorey is dominated by perennial woody shrubs and herbs with the most abundant families being Proteaceae, Papilionaceae, Myrtaceae and Cyperaceae (Bell & Heddle 1989). The climate of the study region is Mediterranean-type with long term average annual rainfall of between 650 - 700 mm yr^{-1} of which approximately 80% falls between the months of May and October. At a nearby (10 km) climate station, over the study period low rainfall years were recorded in 1994 with 451 mm yr^{-1} and 1997 (401 mm yr^{-1}). Higher than average rainfall was recorded in 1992 (717 mm yr^{-1}) and 1996 (753 mm yr^{-1}).

This region contains many remnants of native vegetation of varying size and composition, in a matrix of agricultural land (60% cleared) which is principally maintained for sheep pasture with some cropping. All three chosen vegetation types have a shrub dominated understorey and are characterised by the dominant overstorey species. They include; jarrah and some marri which tend to occur in the mid- to up-slope landscape positions on lateritic gravelly soils in a sandy loam matrix; wandoo which occurs in the shallow valley bottoms on heavier soils; sheoak with an overstorey of jarrah and marri which occur on mid-slopes in sandy soils. For this study, a remnant degraded by continuous livestock grazing was chosen for each vegetation type. Remnants varied in size from 10 to 30 hectares and all of these remnants have been continuously grazed by sheep for at least the last 10 years at stocking rates of approximately 5 sheep per hectare. Grazing pressure tends to be heaviest in summer when there is little feed in the surrounding pasture. For each degraded remnant of each vegetation type, there was a nearby area of intact vegetation that had not been disturbed by livestock grazing, usually separated by a fence or road. Ungrazed remnants of equivalent size to the grazed remnants do not exist in the study area so that ungrazed plots were in larger areas of native vegetation but situated adjacent to cleared agricultural land so that plots would be subjected to similar edge effect disturbances (see Saunders *et al.* 1991).

In grazed remnants of each vegetation type, three paired replicate 10 m x 10 m plots were established. For each pair of plots, one was fenced with a sheep-proof ringlock fence, while the adjacent plot was pegged out and left open. Fencing was effective in excluding sheep but not rabbits and native herbivores. For each vegetation type a further three replicate plots were marked out in an adjacent remnant that had no livestock grazing disturbance. Therefore, for each vegetation type, there were three types of treatment plot, fenced plots in degraded remnants where livestock grazing was excluded, adjacent grazed plots in degraded remnants where livestock grazing has continued and ungrazed plots of native vegetation which have not been subject to livestock grazing disturbance. This gave a total of nine 10 m x 10 m plots in each vegetation type with three fenced, three grazed and three ungrazed plots. Plots were placed approximately 50 m from the boundary of the remnant to minimise edge effects.

The initial vegetation survey of all 10 m x 10 m fenced, adjacent grazed and ungrazed plots was completed in November 1991 with subsequent surveys being carried out annually in November 1992, 1993, 1994, 1995 and 1997. For each survey, all understorey species occurring within a plot were recorded and relative cover-abundance estimated using the Domin-Krajina scale (Mueller-Dombois & Ellenberg 1974). The presence and cover abundance of only the seedlings of overstorey species were recorded and utilised in further analysis. Species diversity was calculated using the Shannon-Weiner index (H) and Sorensen's index of similarity was used (where scores are between 0 and 1 with a score of 1 indicating complete similarity between plots; Kent & Coker 1992) to indicate the degree of similarity between vegetation types and the different treatment plots. A species importance value was calculated for each species in each vegetation type and grazing regime as relative frequency + relative cover.

To identify the effects of grazing on functional types, species were grouped according to life form (*i.e.* native shrubs, native perennial herbs, native perennial grasses, native geophytes, native annual herbs, exotic annual herbs and exotic annual grasses). For the purpose of comparing fenced, grazed and ungrazed plots, cover abundance values were transformed to give equal weighting to each Domin scale class so that plot averages could be calculated. Transformation used the method described by Bannister (1966) where the mean of the combined cover and frequency values can be used to give a transformed linear scale according to $y = 0.0428\ x$.

Results

The ungrazed remnants for each vegetation type are dominated (in terms of number of species) by the families Papilionaceae, Asteraceae and Poaceae including 16 species in the ungrazed wandoo site (Table 1). This is partly due to invasion by exotic weeds. This invasion of weeds is mostly due to other disturbances related to the isolation of remnants such as altered fire regime, increased exposure, and nutrient enrichment (Hobbs & Atkins 1988; Cale & Hobbs 1991; Saunders *et al.* 1991).

In the ungrazed jarrah site 42 families were represented, of which Papilionaceae and Epacridaceae were the most prominent families of native perennial species. At the ungrazed wandoo site there were 39 families, with Cyperaceae and Goodeniaceae being the prominent native perennials. The ungrazed sheoak site had 34 families with the greatest proportion of native perennials in the Proteaceae and Dillieniaceae (*Hibbertia* spp). Plots in the degraded remnants were also dominated by Asteraceae, Papilionaceae and Poaceae with exotic species contributing a large proportion of species, particularly in the Poaceae (Table 1). The lily family Antheriaceae, consisting of native perennial herbs and geophytes, was also prominent in fenced and grazed plots in all vegetation types. For the degraded jarrah site, Stylidiaceae was common in the fenced plots while Orchidaceae was well represented in the grazed plots. There was also an additional 5 native species of Papilionaceae in the fenced plots compared to the grazed plots. Papilionaceae also features in the degraded sheoak plots but only as exotic annual forbs (*Trifolium* spp).

The Sorensen similarity index indicated the floristic similarity between fenced and grazed, fenced and ungrazed and grazed and ungrazed plots for each vegetation type (Fig 1). The greatest similarity was between fenced and grazed plots in 1991 at the time of fencing. Only the fenced jarrah plots have had a significant decline in similarity over the study period ($r^2 = 0.805$, $P = 0.015$). Comparison between fenced and ungrazed plots indicates that only the jarrah plots exhibited significant change towards greater similarity with ungrazed plots ($r^2 = 0.661$, $P = 0.0493$). Similarity between the fenced and unfenced plots and between the grazed and ungrazed plots for the wandoo and sheoak sites have shown no significant trend over time (Fig 1). Between the ungrazed and grazed jarrah plots there is a steady decline in similarity over time ($r^2 = 0.835$, $P = 0.0069$) which indicates that the grazed plots are continuing to degrade (lose species). The similarity between ungrazed vegetation types was 0.38 between

Table 1

Families with the greatest number of species for each of the vegetation types in plots in the ungrazed, fenced and grazed remnants at the time of the initial survey (1991).

Ungrazed Plots

Jarrah	Spp*	Wandoo	Spp*	Allocasuarina	Spp*
Papilionaceae	11 (1)	Papilionaceae	16 (4)	Poaceae	6 (2)
Poaceae	11 (4)	Asteraceae	13 (4)	Asteraceae	5 (1)
Epacridaceae	6	Poaceae	10 (4)	Goodeniaceae	4
Asteraceae	6 (1)	Cyperaceae	6	Dilleniaceae	4
Anthericaceae	6	Goodeniaceae	6	Proteaceae	4

Fenced Plots

Jarrah	Spp*	Wandoo	Spp*	Allocasuarina	Spp*
Poaceae	17 (10)	Poaceae	18 (12)	Poaceae	17 (10)
Asteraceae	14 (3)	Asteraceae	12 (5)	Asteraceae	10 (3)
Papilionaceae	11 (3)	Papilionaceae	11 (3)	Anthericaceae	7
Anthericaceae	8	Anthericaceae	9	Cyperaceae	4
Stylidiaceae	5	Cyperaceae	6	Papilionaceae	3 (3)

Grazed Plots

Jarrah	Spp*	Wandoo	Spp*	Allocasuarina	Spp*
Poaceae	16 (9)	Poaceae	17 (10)	Poaceae	15 (10)
Asteraceae	13 (3)	Asteraceae	15 (5)	Asteraceae	13 (3)
Anthericaceae	7	Papilionaceae	10 (4)	Anthericaceae	4
Papilionaceae	6 (3)	Anthericaceae	10	Papilionaceae	3 (3)
Orchidaceae	4 (1)	Cyperaceae	5	Caryophyllaceae	3 (3)

* number in brackets is the number of exotic species.

jarrah and wandoo, 0.44 between jarrah and sheoak and 0.38 between wandoo and sheoak.

In the fenced jarrah sites there was a trend of increasing species richness over the 7 years with numbers in 1997 similar to the ungrazed site (Fig 2). For the wandoo and sheoak sites there has been little increase in species richness in fenced plots, and species richness is still considerably lower than in ungrazed conditions. Large variance in the degraded remnants (particularly during 1992-93) most likely reflects the fluctuating presence and abundance of annual species as a result of varying annual climatic conditions, principally rainfall. Species diversity shows little trend in the fenced plots for any vegetation type and may therefore be a poor indicator of change with grazing relief due to the influx of exotic species to replace natives and the lack of dominance of any particular species. The generally lower species diversity in degraded remnants compared with ungrazed remnants may reflect the dominance of a few species that are able to tolerate grazing, such as exotic pasture species.

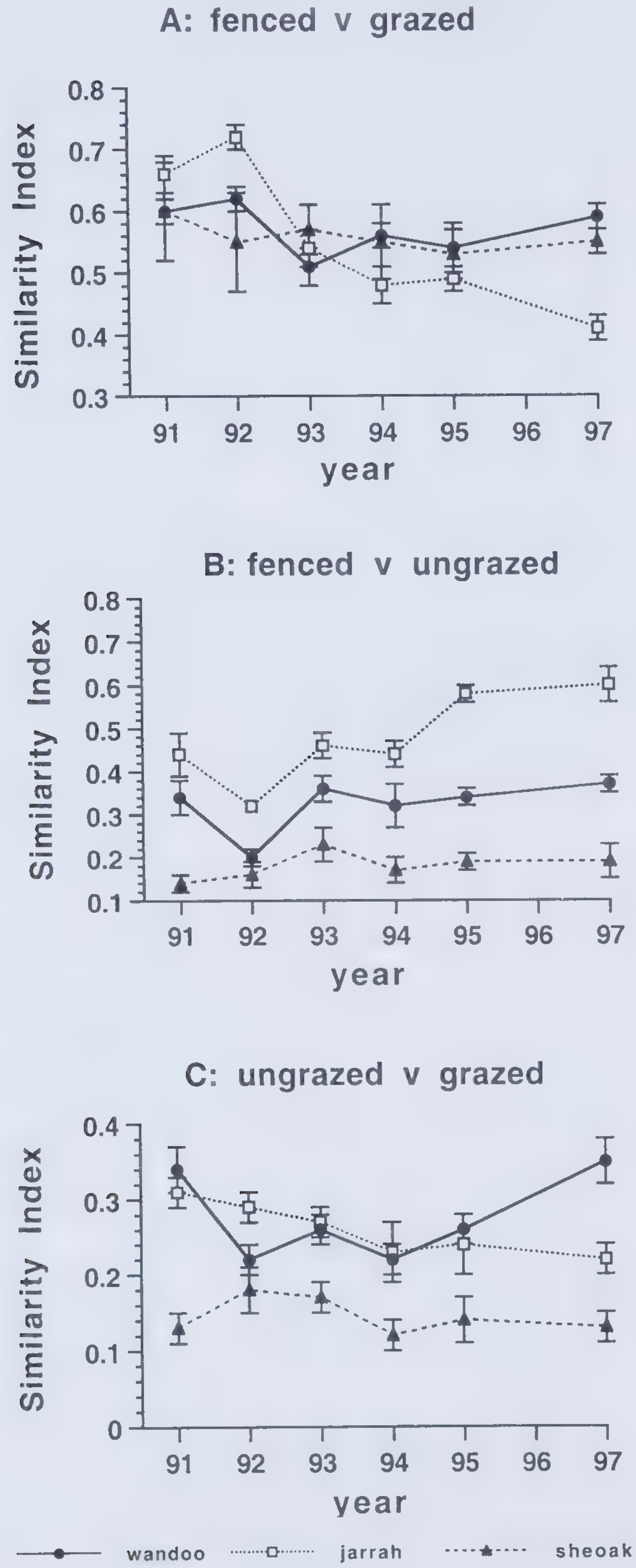

Figure 1. Sorensen similarity index (± se) for comparison of grazed, fenced and ungrazed plots for each vegetation type.

Analysis of species importance shows the dominance of native perennial species in ungrazed plots for all vegetation types, with the 5 most important species contributing from 30% to 40% of the cover (Table 2). In these ungrazed plots, no species are dominant; the only exception is *Dryandra sessilis* in the sheoak plots. In fenced jarrah plots, species importance changed from 4 of the 5 species being exotic annuals in 1991 to 4 of the 5 species being native perennials in 1997. Fenced wandoo plots have continued to be dominated by exotic annual species with only 2 native perennial species becoming important. Fenced sheoak plots have seen the introduction of only one native perennial shrub (*Hibbertia montana*) and continue to be dominated by exotic annual species with the native perennial grass *Neurachne alopecuroidea* becoming important. Grazed plots for all vegetation types are dominated by species such as the exotic annual grass *Aira caryophyllea* and the exotic pasture species *Trifolium campestre* with only the native perennial grasses *Microlena stipoides* (jarrah plots) and *Stipa semibarbata* (sheoak plots) and the native perennial herb *Lagenifera huegelii* being numerically important.

Categorisation of species according to life form revealed a large increase in cover of native perennial grasses, herbs and shrubs in the fenced jarrah plots (Fig 3). Proportions of cover of native geophytes and native annuals have not changed greatly after 7 years of grazing exclusion. By comparison, in the grazed jarrah plots the overall cover has remained low with fluctuating levels of exotic annual species. In fenced wandoo plots there has also been an increase in cover of native perennial herbs and shrubs but also an increase in cover of exotic annuals (Fig 3). Cover in sheoak fenced or grazed plots has not increased significantly over the study period. Cover for life forms in the ungrazed plots for all vegetation types was dominated by native perennial species (Fig 3). Within the jarrah plots these life forms contribute 93% of the cover and 92% and 95% for wandoo and sheoak respectively. These trends in changes of cover for the different life forms in the study plots were also evident in terms of number of species (Fig 4). This indicates that not only has cover of existing species increased but increases in cover have come from the addition of new species into the fenced plots.

Seedlings of overstorey species were recorded in all jarrah plots for all years, with an average of 5 per year in fenced plots, three in ungrazed plots and one in grazed

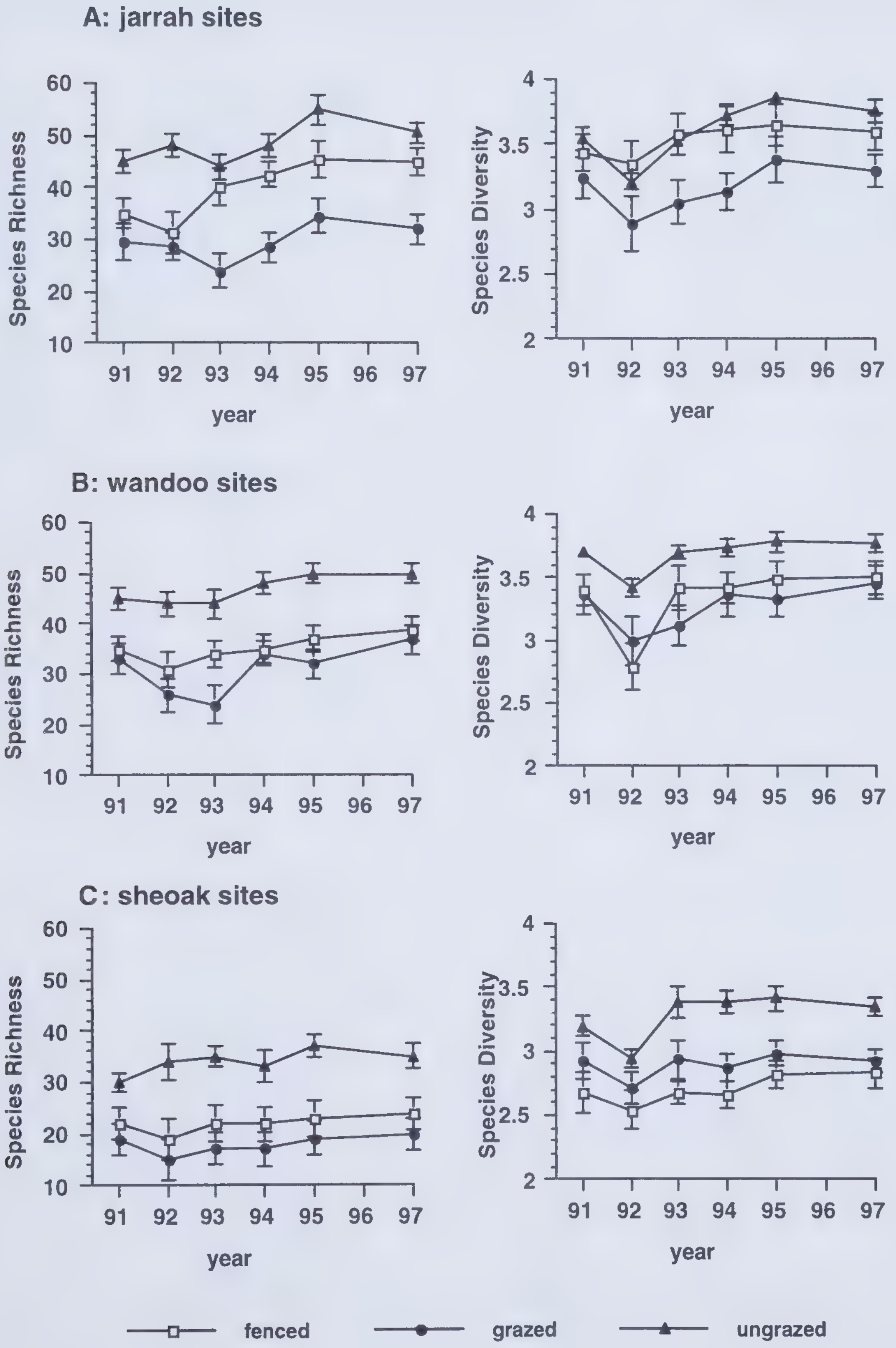

Figure 2. Species richness and diversity (± se) for each of the vegetation types, in grazed, fenced and ungrazed plots over the 7 years of measurement.

Table 2

Species importance value (relative cover + relative frequency) for the 5 highest ranking species for each vegetation type and grazing disturbance recorded for 1991 and 1997.

Ungrazed 1991	Importance value	Ungrazed 1997	Importance value
Jarrah sites		**Jarrah sites**	
Scaevola striata (s)	8.47	*Bossiaea ornata* (s)	12.0
Hakea lissocarpha (s)	7.53	*Lepidosperma gracile* (ph)	12.0
Bossiaea ornata (s)	5.65	*Scaevola striata* (s)	10.3
Trymalium ledifolium (s)	5.65	*Loxocarya fasiculata* (ph)	6.19
Lepidosperma gracile (ph)	3.77	*Trymalium ledifolium* (s)	4.47
Wandoo sites		**Wandoo sites**	
Hakea lissocarpha (s)	11.4	*Lepidosperma gracile* (ph)	10.57
Bossiaea ornata (s)	8.79	*Bossiaea ornata* (s)	10.07
Davesia pectinata (s)	6.72	*Dryandra nivea* (s)	7.89
Lepidosperma gracile (ph)	4.13	*Scaevola striata* (s)	6.88
Hibbertia montana (s)	4.13	*Hibbertia montana* (s)	4.18
Allocasuarina sites		**Allocasuarina sites**	
Dryandra sessilis (s)	29.5	*Dryandra sessilis* (s)	16.72
Bossiaea ornata (s)	8.87	*Bossiaea ornata* (s)	14.49
Hakea lissocarpha (s)	8.87	*Hakea lissocarpha* (s)	14.49
Lepidosperma gracile (ph)	8.87	*Lepidosperma gracile* (ph)	14.49
Glischrocaryon aureum (ph)	8.87	*Glischrocaryon aureum* (ph)	5.02
Fenced 1991		**Fenced 1997**	
Jarrah sites		**Jarrah sites**	
Aira caryophyllea (eg)	22.85	*Lepidosperma gracile* (ph)	10.88
Trifolium campestre (ef)	12.3	*Hypochaeris glabra* (ef)	6.81
Danthonia caespitosa (ng)	11.42	*Scaevola striata* (s)	5.44
Vulpia myuros (eg)	7.91	*Microlena stipoides* (ng)	5.01
Hypochaeris glabra (ef)	5.71	*Gahnia* sp (ph)	5.01
Wandoo sites		**Wandoo sites**	
Trifolium campestre (ef)	26.7	*Trifolium campestre* (ef)	15.67
Kennedia prostrata (s)	8.75	*Bromus diandrus* (eg)	10.3
Aira caryophyllea (eg)	7.44	*Aira caryophyllea* (eg)	9.98
Petrorhagia vellutina (ef)	5.69	*Sollya heterophylla* (s)	6.31
Hypochaeris glabra (ef)	4.37	*Loxocarya flexuosa* (ph)	3.89
Allocasuarina sites		**Allocasuarina sites**	
Hypochaeris glabra (ef)	22.14	*Aira caryophyllea* (eg)	17.65
Vulpia myuros (eg)	19.15	*Trifolium campestre* (ef)	11.67
Aira caryophyllea (eg)	10.17	*Neurachne alopecuroidea* (ng)	11.67
Stipa semibarbata (ng)	9.0	*Vulpia myuros* (eg)	10.94
Helipterum cotula (na)	5.62	*Petrorhagia vellutina* (ef)	10.21
Grazed 1991		**Grazed 1997**	
Jarrah sites		**Jarrah sites**	
Vulpia myuros (eg)	22.76	*Hypochaeris glabra* (ef)	13.83
Aira caryophyllea (eg)	15.52	*Microlena stipoides* (ng)	9.57
Hypochaeris glabra (ef)	11.21	*Aira caryophyllea* (eg)	8.51
Trifolium campestre (ef)	8.01	*Trifolium campestre* (ef)	6.38
Briza minor (eg)	5.17	*Lagenifera huegelii* (g)	6.38
Wandoo sites		**Wandoo sites**	
Trifolium campestre (ef)	12.97	*Aira caryophyllea* (eg)	15.7
Loxocarya flexuosa (ph)	10.57	*Trifolium campestre* (ef)	13.3
Kennedia prostrata (s)	7.75	*Avena fatua* (eg)	11.0
Hypochaeris glabra (ef)	7.52	*Hypochaeris glabra* (ef)	5.89
Aira caryophyllea (eg)	5.64	*Petrorhagia vellutina* (ef)	4.55
Allocasuarina sites		**Allocasuarina sites**	
Stipa semibarbata (ng)	18.42	*Aira caryophyllea* (eg)	26.72
Aira caryophyllea (eg)	11.05	*Stipa semibarbata* (ng)	14.71
Hypochaeris glabra (ef)	11.05	*Vulpia myuros* (eg)	14.71
Vellia trinervis (g)	11.05	*Trifolium campestre* (ef)	10.55
Vulpia myuros (eg)	8.83	*Hordeum leporinum* (ef)	10.1

eg = exotic annual grass; ef = exotic annual forb; g = geophyte; na = native annual forb; ng = native perennial grass; ph = native perennial herb; s = native shrub.

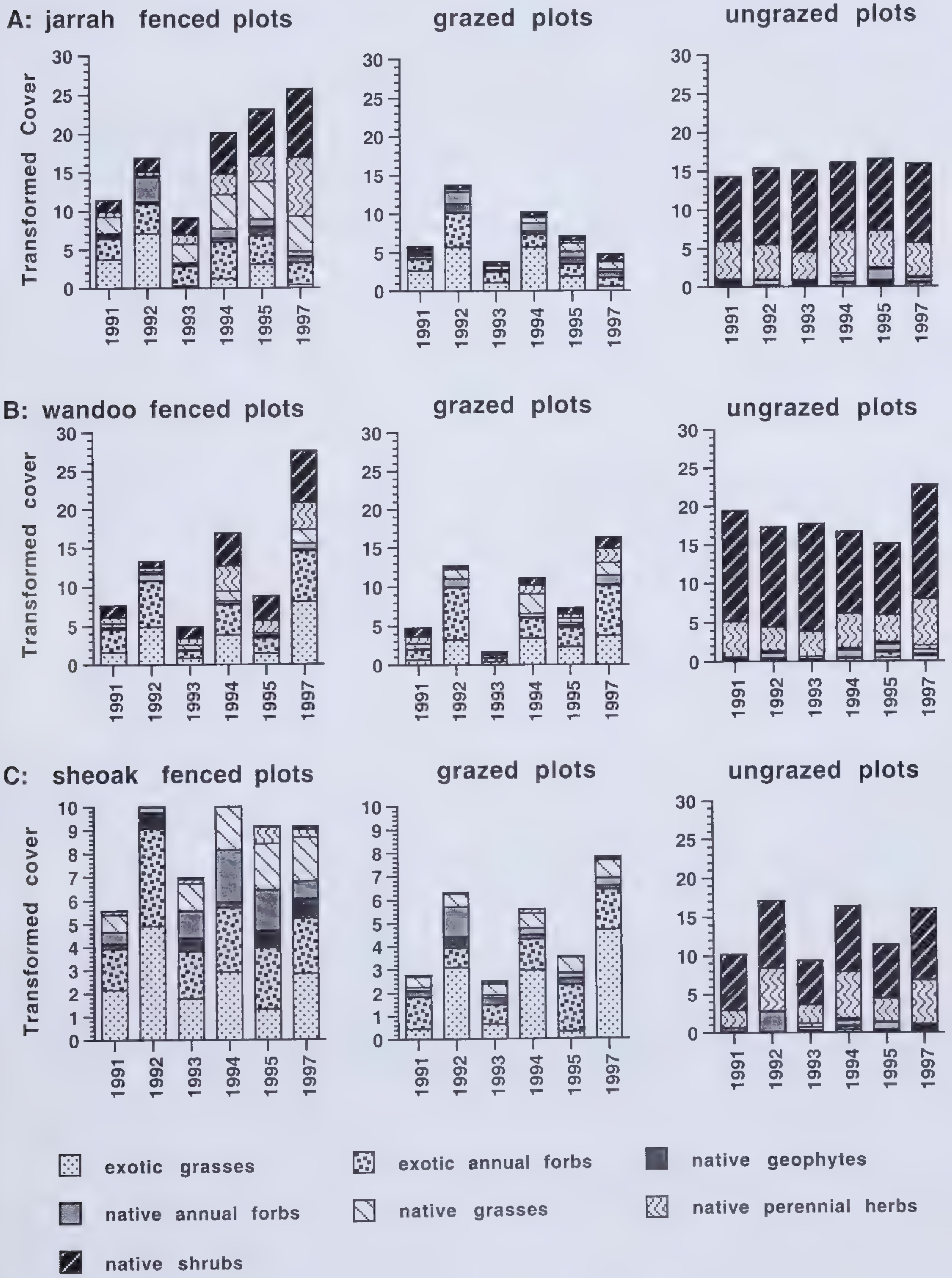

Figure 3. Cover of different life form groups in each of the vegetation types in fenced, grazed and ungrazed plots.

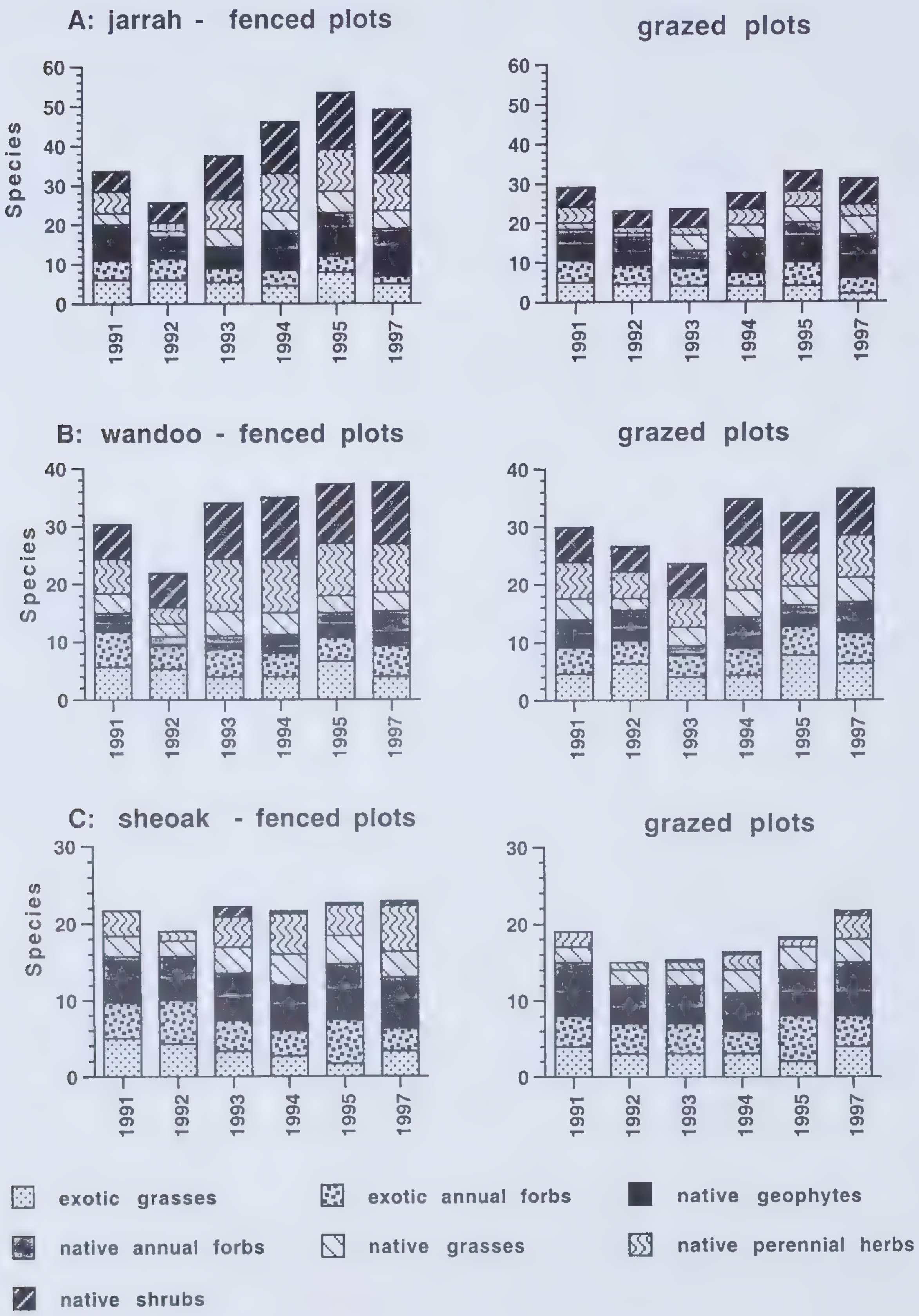

Figure 4. Number of species of different life form groups in each of the vegetation types in fenced and grazed plots. Note the different vertical scale for each vegetation type.

plots. However only at the ungrazed site did seedlings survive into a second or third year. At the wandoo sites, four seedlings were recorded in 1992 in the ungrazed plots; none were recorded in any of the sheoak plots.

Discussion

This study documents the response of the vegetation in degraded woodland remnants in south-west Western Australia, after the cessation of livestock grazing. It also demonstrates the variation in natural regeneration ability of the different vegetation types. Jarrah remnants show a relatively rapid increase in species and vegetation cover of native perennial species after livestock grazing is excluded. Re-establishment of wandoo and, in particular, the sheoak vegetation types, appears to be much slower. However, an important factor in the rate of recovery is the availability of a ready source of reproductive plant material for regeneration. This may come from seed stored in the soil, seed from surviving plants, seed dispersed from surrounding intact vegetation or from vegetative underground storage organs such as a lignotuber which has survived continual grazing of above-ground parts. Our results show that there was a base of existing native perennial taxa in the degraded jarrah remnants and to a lesser extent in the wandoo sites but not at the sheoak sites. Previous work has suggested that on-site soil seedbanks are often not important for natural regeneration of native perennial species in this environment (Vlahos & Bell 1986; Pettit 1995). However, all sites were in close proximity to a source of reproductive material in adjacent ungrazed areas. The mechanisms of seed dispersal from neighbouring sources, such as wind, ants and other vectors, are unclear for most species; however, the species additions recorded at fenced plots were probably derived through seed dispersal. Differences in the ability of native species to re-establish between vegetation types may be due to repression effects on the understorey by both *E. wandoo* (expansive shallow roots; Lamont 1985) and *A. fraseriana* (leaf litter accumulation).

Response of the vegetation to cessation of grazing varies depending on the particular environment, the vegetation type and the grazing history (Milchunas & Lauenroth 1993). In studies of sub-alpine grasslands in eastern Australia, species richness decreased with the exclusion of domestic stock but structural complexity increased (Gibson & Kirkpatrick 1989), herbaceous species and sedges increased in exclosures while shrubs and unpalatable grasses increased in the open plots (Wimbush & Costin 1979) and cover of palatable forbs and shrubs increased substantially with the absence of cattle grazing (Wahren *et al.* 1994). On abandoned farmland in the mallee country in eastern Australia, after initial domination by exotic annuals, some recruitment of understorey shrubs was recorded after 3 years (Onans & Parsons 1980). In *E. salmonophloia* remnants in wheatbelt Western Australia, exclosure plots were dominated by annual exotic species with the regeneration of only one native shrub (Hobbs 1989). The initial increases in annual species in the fenced plots, especially exotic pasture species, have indeed been seen to be only temporary and highly influenced by fluctuations in annual climatic patterns, particularly rainfall distribution and abundance. In remnants degraded by livestock, grazing annual species benefit from grazing due to the increase in area of bare ground that permits establishment and reduces competition from perennial plants which have been removed. The growth phase of annuals is at a time (winter/spring) when there is maximum herbage available, especially in the adjoining pasture, so grazing pressure in remnants is reduced. Other life form groups such as geophytes and native perennial grasses also benefit in this regard because they are unobtainable by livestock during the time of greatest grazing pressure (late summer). The rapid growth of resprouting shrubs and perennial herbs may also make them able to compete successfully with the exotic weeds (Keeley 1986; Hansen *et al.* 1991). However, resprouters need time to recover starch reserves so that they can resprout (Bowen & Pate 1993). Frequent or persistent grazing therefore can exhaust reserves and eventually lead to their loss. Species relying on seed for regeneration can persist only as long as seed is available in the seedbank or is brought in from an outside source. Lack of regeneration of perennial shrubs in the sheoak plots would suggest that possibly the store of perenniating organs and seed has been exhausted.

Germination of seed of overstorey species was recorded in the fenced, grazed and ungrazed plots in this study, but survival of seedlings and saplings has been minimal and only in ungrazed and fenced plots. Greater regeneration of overstorey species may be a factor of parental seed source, favourable climatic conditions and a disturbance creating a recruitment opportunity. Recruitment of jarrah seedlings is enhanced by reduction of soil moisture deficit in late spring and summer, removal of litter and ground cover and some soil disturbance (Stoneman *et al.* 1994). The successful recruitment of wandoo requires a hot fire to create ashbeds for seedling establishment (Burrows *et al.* 1990).

At a relatively early stage of decline in a remnant, the structure and composition of the native community can be re-established by excluding stock. However, under severe and prolonged grazing, the lignotuber bank of resprouters and the seedbank of seed regenerators has been lost and regeneration will be more difficult. Our results indicate that the degree of difficulty will vary for different community types even within the broad category of jarrah and wandoo woodlands. Therefore, consideration of vegetation type is an important factor when managing for the restoration of remnants of native vegetation. This also raises the question of whether intervention such as reseeding, replanting or weed control is required to enhance the natural regeneration process. Natural regeneration may still take place in communities such as the wandoo and sheoak remnants but may take much longer to become evident. The duration of livestock exclusion monitored in this study (7 years) is still a relatively short period, especially if recruitment is episodic and requires a confluence of climatic and disturbance factors. Continued long term monitoring is required to assess this.

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Myrtaceous shrub species respond to long-term decreasing groundwater levels on the Gnangara Groundwater Mound, northern Swan Coastal Plain

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Abstract

Analysis of four vegetation transects that were established on the Bassendean Dune System, northern Swan Coastal Plain classified 42 native plant species into four 'habitat' groups based on their preferred soil moisture regimes (Havel 1968). Using adult abundance and distribution data from three of these transects and an additional transect established in 1976, we investigated the various ecological responses of myrtaceous shrub species representing the four habitat groups to long-term (20-30 yr) decreasing groundwater and soil moisture levels. Myrtaceous shrubs were chosen for analysis because of their widespread occurrence and diversity on the Swan Coastal Plain, and because Myrtaceae is the only plant family to be represented in all four of Havel's habitat categories. Myrtaceous species 'tolerant of excessive wetness' (*Astartea fascicularis, Hypocalymma angustifolium, Pericalymma ellipticum, Regelia ciliata*) are all shallow rooted (rooting depth < 1m), occur in winter-wet depressions, and displayed the greatest reduction in population size in response to decreasing groundwater levels. Species cateogorised as displaying 'maximum development on dry sites' (*Eremaea pauciflora, Melaleuca scabra, Scholtzia involucrata*) commonly occurred on the upper and mid-slopes of the transects, are deeper-rooted and varied in their population response to long-term declines in water availability. All three species probably rely to some extent on accessing soil moisture at depth (2-6 m) during summer drought. The scenario was similar for species 'optimum on moist sites' (*M. seriata*) and for species 'without clear-cut site preferences' (*Calytrix flavescens*). In the context of Havel's four habitat categories, whether a particular habitat preference is 'wet' or 'dry' refers to availability of soil moisture, although to what soil depth and moisture levels are uncertain. Habitat preferences, based on soil moisture availability, may have no relevance to a species preferred groundwater regime and hence response to decreasing groundwater levels. A species' groundwater requirements during periods of drought are dependent on their position in the landscape, summer groundwater depth and the species rooting depth.

Introduction

In the mid 1960s, an investigation into site (habitat) preferences of a range of native species from Bassendean Dune System of the northern Swan Coastal Plain (Havel 1968) related seasonal variations in soil moisture, and depth to confining layers (*e.g.* coffee rock) to species distribution along several transects positioned to cover a range of topographical scenarios. Using these data, species were classified as either being

1) tolerant of excessive wetness;

2) optimum on moist sites;

3) maximum development on dry sites; and

4) without clear-cut site preferences.

Overall, 10 overstorey (mainly *Banksia* and *Eucalyptus*) and 32 understorey species were included in the analysis.

The Bassendean and other dune systems form part of the northern Swan Coastal Plain, under which lies a large, shallow unconfined aquifer, the Gnangara Groundwater Mound. Groundwater and soil moisture levels have been gradually decreasing in most areas of the Mound since the 1970s as a combined result of several years of below average rainfall and increased groundwater abstraction (Davidson 1995). Species that, according to Havel (1968), are found in low lying, seasonally waterlogged areas (*e.g. Astartea fascicularis, Pericalymma ellipticum*) may not be able to tolerate decreasing groundwater levels due to their typically shallow root systems (Dodd *et al.* 1984). In contrast, deeper-rooted shrub species usually rely on groundwater sources for most, if not all, of the year, depending on their position in the landscape (depth to groundwater) and a species maximum rooting depth. In response to decreasing groundwater levels, these species may be forced to compete for soil moisture sources at depth. Both soil moisture and groundwater levels are dependent on recent rainfall events and evapotranspiration rates (Farrington & Bartle 1989), with the rise and fall of the water table depending on the movement of the wetting front and decreasing soil water storage respectively in the soils unsaturated zone.

The family Myrtaceae is well represented on the Gnangara Groundwater Mound, mainly consisting of small shrubs (24 species from 12 genera), but also *Eucalyptus* (4 species) and *Melaleuca* (2 species) trees. The many damplands are often surrounded by a shrub stratum of *Astartea fascicularis* and *Pericalymma ellipticum* in areas prone to waterlogging; species such as *Hypocalymma angustifolium* and *Regelia ciliata* are dominant along the upper edges of these depressions where the soil is rarely waterlogged (Farrington *et al.* 1990; Muir 1983). In elevated postions (upslope) deeper-rooted species (*e.g. Eremaea pauciflora, Calytrix flavescens*) are common. Their great diversity and widespread occurrence on the Mound makes the myrtaceous shrubs an ideal group of species to study changes in species distribution and abundance, in relation to long-term variations in groundwater levels and known site preferences. The Myrtaceae is also the only family to be represented in all four of Havel's habitat categories. To determine the ecological significance of these groups in response to long-term groundwater fluctuations and soil moisture levels, we examined data for selected myrtaceous shrub species (those mentioned by Havel 1968) collected over a 20-30 year period along topographical, and hence depth to groundwater, gradients.

Methods

Study area

The Gnangara Groundwater Mound, bounded by the Swan River (south), Moore River and Gingin Brook (north), Darling Scarp (east) and the south-west Australian coast (Allen 1981), underlies seasonal and permanent wetlands, pine plantations and extensive areas of native *Banksia* woodlands of the northern Swan Coastal Plain. The Mound is one of two large, shallow unconfined aquifers on the plain, and is recharged directly by rainfall. The vegetation of the three main dune systems (Bassendean, Spearwood and Quindalup) is dominated by a *Banksia* overstorey with the occasional *Eucalyptus* and *Allocasuarina* stand, and an understorey consisting mainly of low shrubs from the Myrtaceae, Fabaceae and Proteaceae. The many seasonal damplands, swamps and permanent wetlands are often fringed by *Banksia littoralis* and *Melaleuca* tree species with a variable understorey consisting of species mainly from the Cyperaceae, Juncaceae and Myrtaceae (Semeniuk *et al.* 1990). The distribution of vegetation on the northern Swan Coastal Plain is predominately determined by the underlying landforms, soils, depth to water table and climatic conditions (Heddle *et al.* 1980; Cresswell & Bridgewater 1985). The Mound experiences a dry mediterranean-type climate (Beard 1984), with hot dry summers (December-March) and cool wet winters (June-August) with an average of 870 mm annual rainfall recorded at the Perth meteorological station.

Table 1

Myrtaceous shrub species occurring within the four study transects, listed according to their habitat preferences as determined by Havel (1968). Rooting depths were obtained from Dodd *et al.* (1984) where shallow roots are < 1 m, medium roots are 1- 2 m, and deep roots are > 2 m.

Species	Rooting depth
Tolerant of excessive wetness	
Astartea fascicularis (Labill) DC	shallow
Calothamnus lateralis Lindley	shallow
Hypocalymma angustifolium (Endl) Schauer	shallow
Pericalymma ellipticum (Endl) Schauer	shallow
Regelia ciliata Schauer	shallow
Maximum development on dry sites	
Eremaea pauciflora (Endl) Druce	deep
Melaleuca scabra RBr	deep
Scholtzia involucrata (Endl) Druce	medium
Optimum on moist sites	
Melaleuca seriata Lindley	deep
Without clear-cut site preferences	
Calytrix flavescens Cunn	deep

Vegetation transects

Four vegetation transects (including South Kendall, Neaves and Tick Flat; see Fig 1) were established in 1966 (Havel 1968) to assess the use of native species as indicators of suitable areas for growing pine plantations, and were positioned in areas where both existing pine plantation and relatively undisturbed native vegetation occurred side by side. These transects were resurveyed in 1976 (Heddle 1980), following the commencement of abstraction from public groundwater production bores. A transect were established near Lake Jandabup in 1976 in response to concerns about decreasing groundwater levels on the fringing native vegetation. Each transect contained at least one myrtaceous species (see Table 1) from 3 of the 4 habitat preferences listed by Havel (1968).

All transects were subsequently monitored on a tri-annual basis during September-October (spring) of the designated year. Transects were located along a topographical gradient, incorporating a dampland, wetland or local depression (low lying area) and terminating at a dune crest. They consisted of two parallel 20 m wide lines varying in length between 200 and 500 m. Each line was subdivided into 20 m x 20 m plots for assessment of overstorey composition, within which two 4 m x 4 m plots were used to assess the composition and abundance of understorey species. Fires have been relatively uncommon, with 2 or 3 fires occurring within each transect between 1966-1996.

Neaves (31°42′ S, 115°53′ E), Lake Jandabup (31°45' S, 115°51' E) and South Kendall (31°47' S, 115°52' E) transects were located on the southern part of the Mound (Fig 1), within 10 km of each other, with Neaves and South Kendall the only transects currently under the direct influence of groundwater drawdown resulting from the nearby Wanneroo and Mirabooka borefields respectively. The Tick Flat transect (31°24' S, 115°42' E) in the north (Fig 1), is not directly influenced

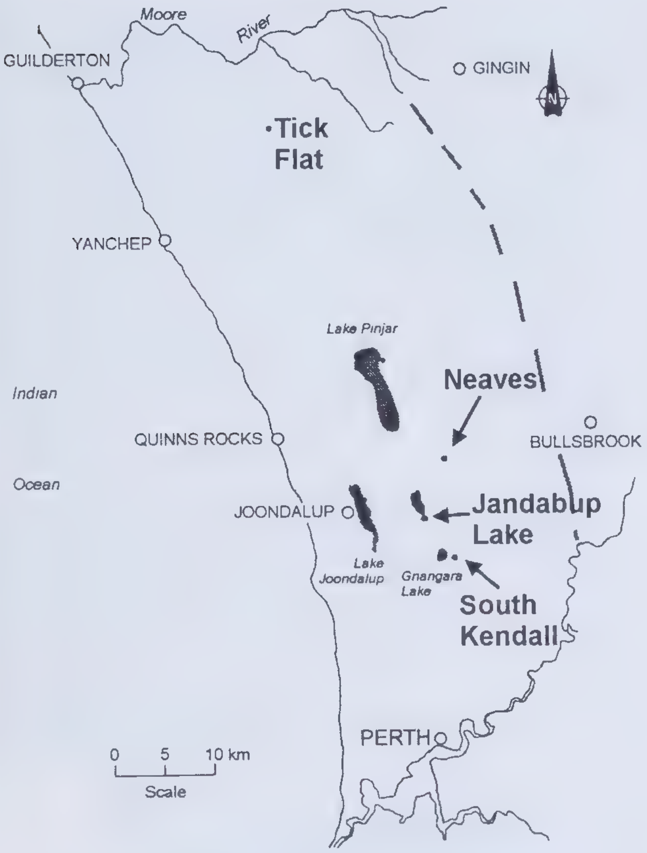

Figure 1. Location of four long-term vegetation monitoring transects (Lake Jandabup, Neaves, South Kendall, Tick Flat) on the northern Swan Coastal Plain, in relation to town sites and local lakes. Eastern boundary of coastal plain is represented by a dashed line.

by abstraction due to its great distance from any existing borefields.

Species distribution, groundwater and soil moisture

Abundance (number of adult plants) and distribution data along the transects for each species under investigation (Table 1) were compiled over approximately 10 year intervals from floristic data collected by J Havel, and Mattiske Consulting Pty Ltd, (unpublished data) between 1966-1996. Only distribution data were available for those transect monitored in 1966 (Neaves, South Kendall, Tick Flat).

Relating species distribution and changes in adult abundance to past groundwater levels experienced by the transects could not be achieved, because the transect's groundwater levels were not monitored. Instead species response to past groundwater regimes were analysed from hydrographical data obtained from the closest groundwater monitoring bore to the transects (usually about 1 km away from a transect) from a database maintained by the Water and Rivers Commission. Groundwater depths within the transect were measured in June 1998 using a hand auger every 30 m along the transects up to a depth of 10 m.

Soil samples were collected with a hand auger at 20 cm intervals to 3 m soil depth, every 20 m along the transects during each vegetation survey, and the moisture content measured gravimetrically. Perth's annual rainfall data since 1960 was obtained from the Western Australian Bureau of Meteorology.

Results

Groundwater levels

The annual hydrological cycle observed at monitoring bores within the vicinity of the four transects are typical of the hydrology of the Western Australia's Swan Coastal Plain. Maximum groundwater depth occurred in March-April resulting from a 3-4 month period of hot summer drought (Fig 2). The main recharge, and minimum groundwater depths, occurs during the winter and spring months (April-October).

Since 1976, groundwater monitoring bores near the four vegetation transects have shown a gradual decrease in groundwater levels (Fig 2A), resulting from several years of below average rainfall (Fig 2B). This decrease was greatest near Neaves and Tick Flat, where the maximum groundwater drawdown during the 20 year period was approximately 2 m, compared with less than 1 m for South Kendall and Lake Jandabup. Between 1979-1985, Perth experienced several years of below average (<870 mm) rainfall (Fig 2B) resulting in a 0.4-0.8 m drop in groundwater levels at monitoring bores near Tick Flat,

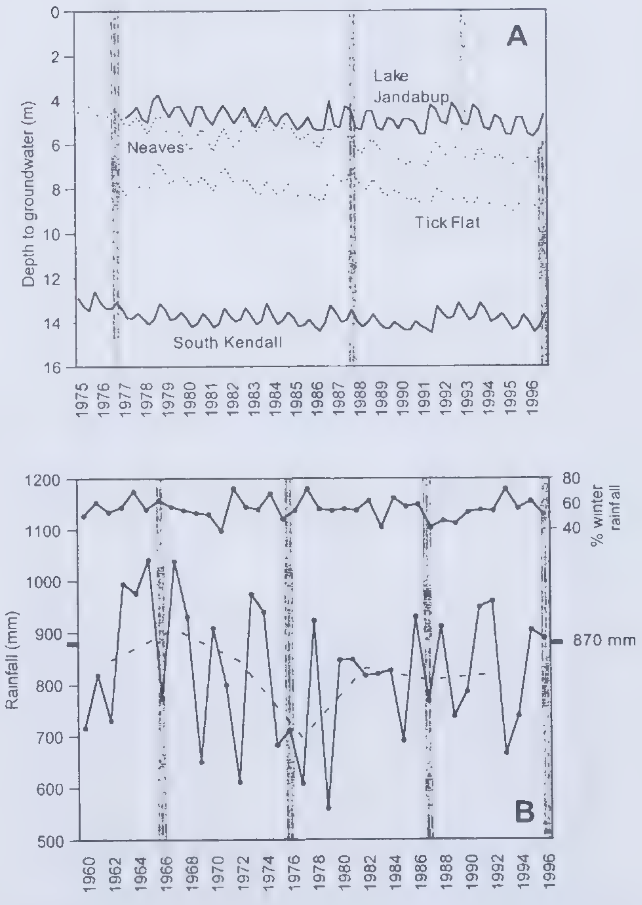

Figure 2. A: Hydrographs from the closest groundwater monitoring bores to the four vegetation transects. B: total (solid line), 5 yearly mean (dashed line) and winter contribution to Perth's rainfall from 1960-1996. Perth's long term average annual rainfall is 870 mm. Bars represent years when transects were monitored.

South Kendall and Lake Jandabup. For all transects groundwater recharge, calculated as spring (maximum) minus preceding autumn (minimum) groundwater depth, ranged from 0.5-0.8 m on average between 1979-1985.

Comparing 1976-1986 with 1987-1996 groundwater data, mean annual minimum groundwater depths decreased by 1.2 m for Neaves but only 0.1 m at Tick Flat. In comparison, groundwater depths decreased by 0.2 and 0.4 m at South Kendall and Lake Jandabup respectively. There was no significant difference in the mean annual groundwater recharge between or within sites over the two 10 year periods. Below average rainfall in 1989 and 1990 (750 and 790 mm respectively) caused a decrease in water levels in 1991 at all four monitoring bores as a direct result of poor groundwater recharge.

Soil moisture

Profiles of soil moisture content show that in spring (October) 1966, groundwater occurred within 3 m of ground level somewhere (usually the lower areas) on all four transects (Fig 3). Soil moisture content >20% indicated that the soil sample was obtained from or below the groundwater table (Havel 1968). By 1976, soils at both 1 and 3 m depth were drier at all sites, with the exception of Lake Jandabup where a significant proportion of the transect is influenced by the adjacent wetland water levels. Eleven years later, a soil moisture content > 20% was not detected at either Neaves or Tick Flat. Overall there was a decreasing trend in soil moisture content over the 30 year period. Soil samples used to calculated moisture content were collected in years where rainfall was more than 100 mm below (1966, 1976, 1987) or just above (1996) the average. The year 1976 had the lowest annual rainfall (711 mm) with winter rainfall accounting for 48% of the annual total. In comparison, winter rainfall accounted for 62% of the total in 1996. However, higher annual rainfall does not necessarily imply a greater contribution of winter rainfall (Fig 2B).

Species abundance and distribution

Half of the myrtaceous species studied were shallow-rooted and classified as tolerant of excessive wetness (Table 1). In 1966, these species were confined to the lower end (both in terms of topography and groundwater depth) of the transects (Fig 4), with *Astartea fascicularis* (only 1 individual) and *Hypocalymma angustifolium* at Tick Flat being the exceptions. In 1976, the distribution of these species had moved further upslope at South Kendall and Tick Flat (but not Neaves).

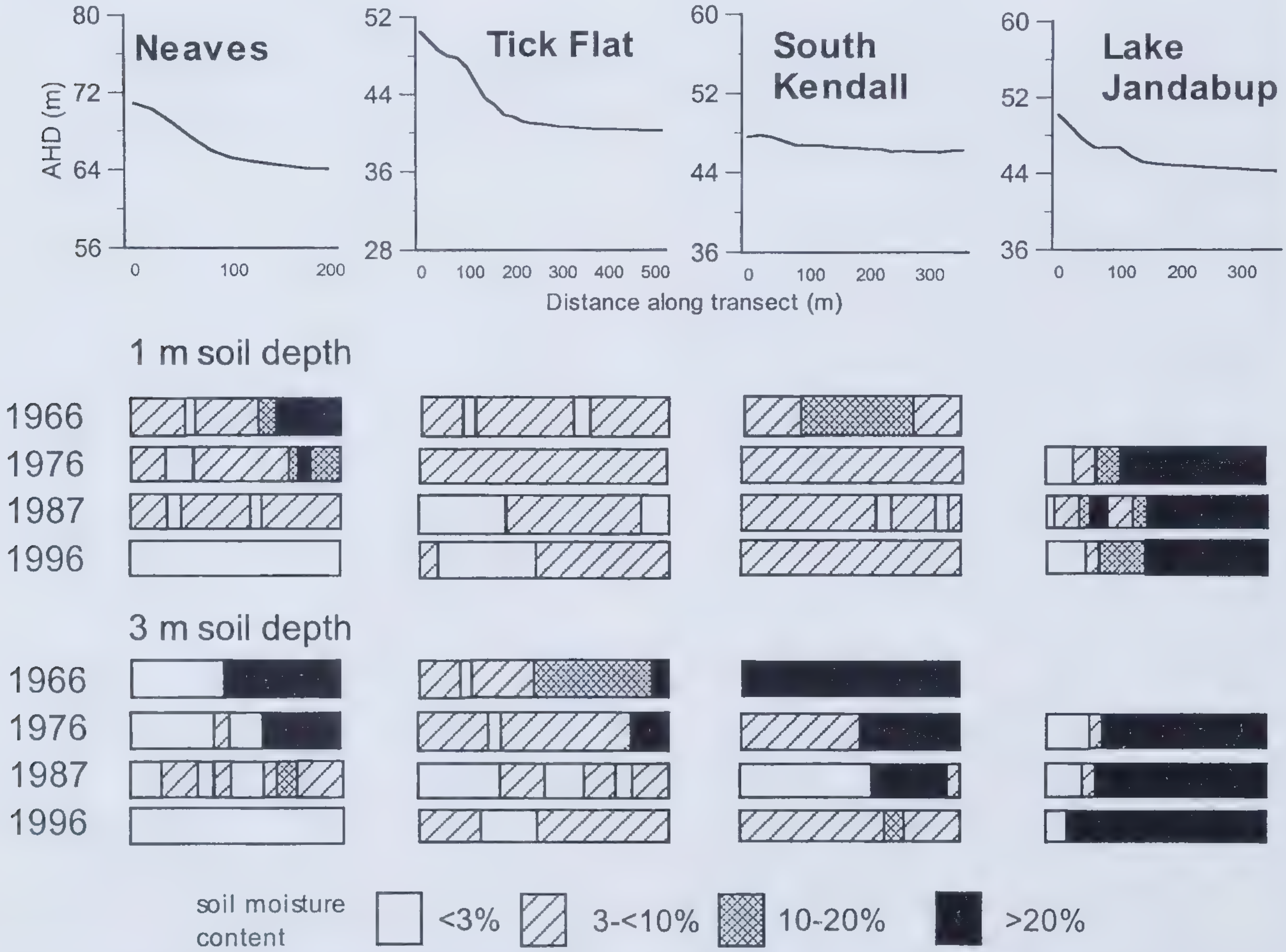

Figure 3. Spring (October) soil moisture profiles along the four transects at 1 and 3 m soil depth between 1966-1996. For the Lake Jandabup transect, the most recent soil moisture data was collected in 1993 (not 1996). Transect topography provided for comparative purposes. Soil moisture data collated from Heddle (1980) and unpublished sources.

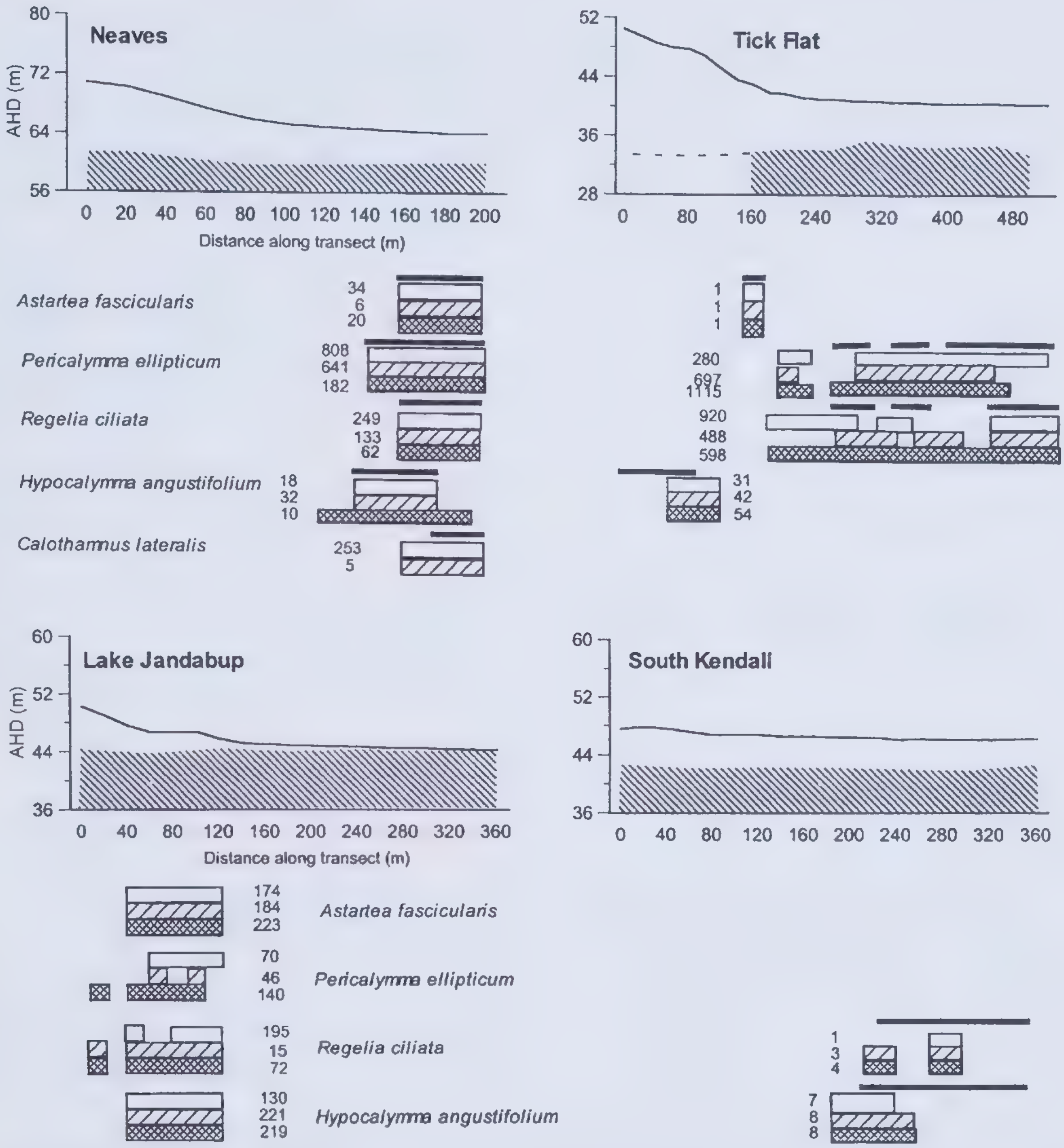

Figure 4. Distribution and abundance of myrtaceous shrub species 'tolerant of excessive wetness' within the four transects. Data shown for 1966 (thick solid line), 1976 (non-shaded bar), 1987 (light cross-hatching) and 1996 (dense cross-hatching). Transect topography and groundwater depth profiles are provided for comparative purposes. Groundwater data was collected in August 1998.

From 1976 onwards, only minor changes in the distribution of these 'excessive wetness' species were recorded within the four transects. At Neaves, the number of *Pericalymma ellipticum*, *Regelia ciliata* and *Calothamnus lateralis* plants decreased significantly between 1976 and 1996, with *C. lateralis* not found in the transect by 1996. The total number of adult plants increased for *P. ellipticum* and decreased for *R. ciliata* at Lake Jandabup and Tick Flat. *Hypocalymma angustifolium* also increased in their abundance at these two transects, with no change in their distribution. The number of *P. ellipticum* and *R. ciliata* plants at South Kendall were < 9 throughout the 20 year monitoring period.

Melaleuca seriata, the only myrtaceous shrub species classified by Havel (1968) as being 'optimum on moist sites' occurred at three of the four transects in various positions along the landscape (Fig 5), decreasing in numbers at Neaves and Tick Flat (shift in distribution or removed from transect) and South Kendall (no change in distribution) by 1996. The three species classified as 'wide tolerance, maximum development on dry sites' occurred on the mid- and upslopes of the transect (Fig 5). *Eremaea pauciflora* had decreasing numbers at all sites where it occurred with only a slight change in their distribution along the transect, although at Jandabup and Tick Flat the numbers were always < 11. *Scholtzia involucrata* had a disjunct distribution at South Kendall and Tick Flat, with the most significant changes in distribution patterns occurring between 1966 and 1976. *Calytrix flavescens*, the only myrtaceous shrub species to be classified as 'without clear-cut site preferences', occurred almost along the entire length of

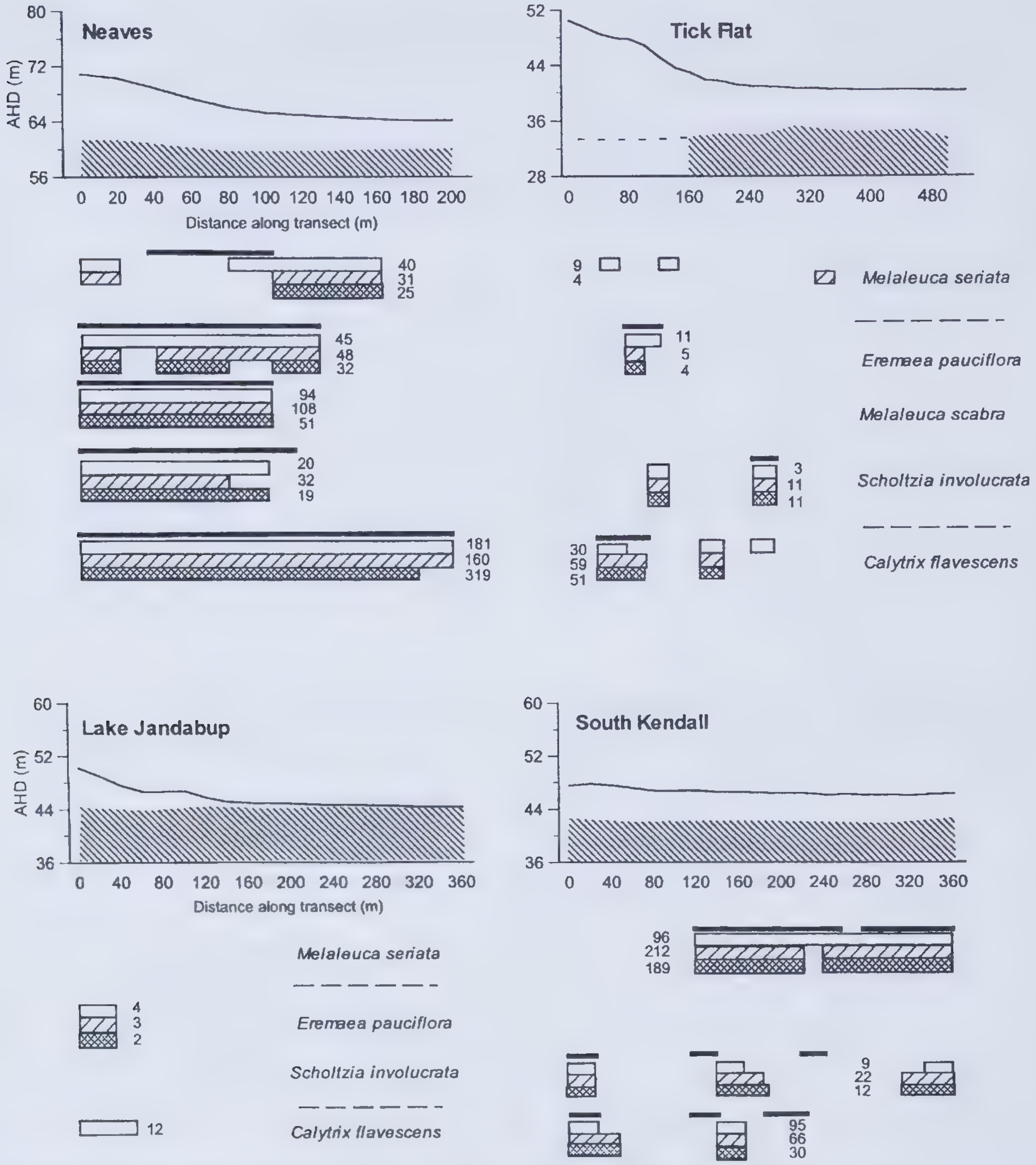

Figure 5. Distribution and abundance of myrtaceous shrub species that display 'optimum on moist sites' (*Melaleuca seriata*), 'maximum development on dry sites' (*Eremaea pauciflora, M. scabra, Scholtzia involucrata*), and with 'no clear-cut site preferences' (*Calytrix flavescens*) within the four transects. See Figure 4 for further details.

the Neaves transect, but was lost from Jandabup by 1987. Between 1966 and 1976, the distribution of *C. flavescens* decreased (South Kendall) or increased (Tick Flat). At Neaves the number of individuals of *C. flavescens* almost doubled between 1976 and 1996.

Discussion

Neaves was the only transect currently under the influence of borefield abstraction to show any significant change in myrtaceous shrub species abundance since abstraction began on the Gnangara Groundwater Mound. The influence of groundwater drawdown was not confined to any particular species group, but was more prominent for those species 'tolerating excessive wetness'; however, the decrease in abundance was not caused by a change in their topographical distribution. Long-term reduction in groundwater levels at Neaves, resulting from the combined effects of poor groundwater recharge and increased groundwater abstraction, is the most likely cause of the decline of these shallow-rooted 'excessive wetness' species, resulting in the species succumbing to the continual water deficit pressures during the dry summer periods. These species may have been dependent on groundwater sources during the 1960's and early 1970's when groundwater depths were shallower. Groundwater levels in 1976 were estimated to be between 1-2 m (Heddle 1980), at the lower end of the transects compared with current levels (2-6 m). As groundwater levels receded only individuals capable of maintaining root growth, or surviving on limited soil moisture reserves, survived. Depth to groundwater fluctuations was not considered to be an important factor influencing the distribution of myrtaceous shrub along the South Kendall transect (also under the influence of abstraction), due to its relatively flat landscape (extending 220 m) rising to a small dune crest.

The dominant shrub species in winter-wet depressions on the Swan Coastal Plain are shallow-rooted, myrtaceous species (Muir 1983). Indeed all the species studied in this paper classified as 'tolerating excessive wetness' occur in low lying areas of relatively shallow groundwater depths, that during the winter months, may sustain high soil moisture levels within the unsaturated zone. However, *Astartea fascicularis* and *Hypocalymma angustifolium* were also located in areas upslope from these localised depressions, suggesting the presence of 'coffee rock', a ferruginous confining layer that can cause water tables to be perched. The five species mentioned in this paper may be able to tolerate 'excessive wetness', but also occur over a range of groundwater depths (1 to 9 m, in 1998) which may not be currently prone to excessively wet conditions. The ability of these species to tolerate 'wet' conditions, must be ultimately be viewed in the context of seasonal fluctuations in water availability, position within the landscape, underlying geology, and groundwater depths. Ecophysiological responses to soil-drying and a lowering water table during summer may be more important in explaining the distribution of these species on the Mound. However we can not discount the influence of fire on the adult populations of these shallow rooted species. Adults of *Pericalymma ellipticum* and *Regelia ciliata* are killed by fire, whereas adults of *A. fascicularis* and *H. angustifolium* recover from underground rootstocks (Dodd *et al.* 1984; B Lamont, Curtin University, *pers. comm.*). All other myrtaceous shrub species mentioned in this paper have the capacity to resprout after a fire (B Lamont, *pers. comm.*).

Species categorised as 'maximum development on dry sites' commonly occurred on the upper and mid-slopes of the transects. For the medium-rooted *Scholtzia involucrata*, Dodd *et al.* (1984) described its response to periods of summer drought to be similar to that of co-occurring shallow-rooted species (*i.e. Hibbertia subvaginata*), although the level of water stress incurred was less severe. This may be due to the ability of medium-rooted species to access soil moisture at depths unavailable to species with shallower root systems. Soil moisture seems to be the only source of water available to *S. involucrata*, as none of the transects had groundwater levels < 2 m where this species occurs, even accounting for past hydrological fluctuations. Despite an overall reduction in soil moisture since 1976 along the transects, the number of individuals increased or did not change.

The remaining species in the 'dry sites' category were deep-rooted, with root depths > 2 m. At a groundwater depth of 7 m, low xylem pressure potentials during summer indicated that the root system of *Melaleuca scabra* were not in contact with the water table (Dodd & Bell 1993). Based on this information, Dodd & Bell (1993) suggested that the maximum rooting depth of *M. scabra* was between 3-4 m and utilized soil moisture stored at these depths. A similar explanation was used for *M. seriata*, a species 'optimum on moist sites'. For both these species, water stress during drought is caused by gradual exhaustion of soil moisture storage at depth, which for *M. seriata* at Neaves and Tick Flat resulted in a shift towards shallower groundwater depths, or loss from the transect. A similar ecophysiological scenerio may also occur for *Calytrix flavescens* (Dodd *et al.* 1984), the only myrtaceous shrub species cited by Havel (1968) as having 'no clear-cut site preference'. *Eremaea pauciflora* (a 'dry site' species) is considered to function as a phreatophyte until the onset of summer drought (Dodd & Bell 1993). In their study, Dodd & Bell (1993) showed that for *E. pauciflora* the critical depth at which the water table apparently fell beyond the reach of the root systems, resulting in water stress, was 6.5 m (at an annual depth to groundwater ranging from 6-7 m). Groundwater levels falling below the reach of the root systems may have been responsible for the long term decline observed in *E. pauciflora* populations.

The concept of 'wet' or 'dry' habitat preferences mentioned in this paper relates to soil moisture levels up to 3 m depth, as described by Havel (1968). Whether a particular location on the landscape is 'wet' or 'dry' is presumably dependent on the presence of soil moisture throughout the year, although the critical soil depth and moisture levels are uncertain. On the deep sands of the Swan Coastal Plain, soil moisture levels are strongly in phase with the seasonal pattern of rainfall up to 10 m depth (Sharma & Craig 1989). Groundwater levels are closely tied to rainfall events, which in turn, are directly related to soil moisture levels. Typically water levels rise in response to a rainfall event soon after the wetting front has reached the groundwater. At relatively shallow soil depths (3-5 m) the soil profiles progressively dries out by evapotranspiration during summer, once significant rainfall ends in spring, reaching a minimum moisture level by autumn (Farrington & Bartle 1991). Beyond 10 m depth, evapotranspiration is non-existent due to a lack of plant root activity (Sharma & Craig 1989). Recharge within *Banksia* woodlands on the Gnangara Groundwater Mound has been calculated to be 10-43% of annual rainfall (Carbon *et al.* 1982; Farrington & Bartle 1989; Sharma & Craig 1989; Sharma *et al.* 1991), with the recharge rate varying with changes in land use, topography and soil type.

Whether a species prefers 'wet' or 'dry' habitats is not directly related to groundwater depth preferences, and depends on the plant species in question. Shallow rooted shrub species at relatively shallow depths to groundwater, may utilize both water sources depending on the degree to which water levels drop over summer. At deeper depths these species rely exclusively on soil moisture sources all year round. In contrast, deep rooted species may rely on groundwater sources during the dry summer months reverting to soil moisture when groundwater sources become unavailable. The habitat groups defined by Havel (1968) do provide valuable ecological information on a selection of Swan Coastal Plain species; however they may not be useful indicators of long term changes in groundwater levels or soil moisture at depth.

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Tektites - the age paradox controversy revisited

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Abstract

The australite age paradox controversy of the 1970's is revisited in the light of recent developments in our knowledge of tektites. Important new discoveries in the North American and other strewn fields provide strong, but indirect evidence against the very young (<20 000 years) age of arrival for australites to the Australian continent proposed by Baker (1959, 1962), Gill (1970) and Lovering *et al.* (1972, 1979). Though the evidence from the Lake Torrens region of South Australia presented by these authors at the time was extremely convincing, the evidence from outside Australia is such that to accept this young age of arrival seems to require acceptance of an impossible set of corollaries. The 0.77 myr radiometric age of the tektites must, it is believed, be the age of return to Earth of the terrestrial-sourced australites, though this implies a "dark age" in the geological history of the tektites of which we have no knowledge and also extraordinary preservation through three quarters of a million years of some almost pristine ablated flanged forms in four regions of Australia. Microtektites are found in deep-sea sediments offshore from Australia of the radiometric age and none are found of the suggested younger age. It is suggested that direct evidence of tektites or microtektites within older Pleistocene formations might be revealed in hidden sections of unconsolidated sediments beneath the large saline claypan lakes south of Kalgoorlie (though the technical difficulties of studying such sections are immense, and the Pleistocene representation there appears to be thin). Direct evidence supporting the radiometric age has lately come from the Bow River area in the north of Western Australia and from a re-examination of the stratigraphy near Port Campbell, Victoria. It seems likely that ablated tektites, those which have exited from and re-entered the Earth's atmosphere, are restricted to the distal part of the Australasian strewn field, south of a boundary line running just north of Java.

Introduction

A recent review of the global occurrence of tektites (McCall 1997) concluded that the two outstanding unsolved enigmas of Australasian tektite origins are (1) the source of the Australasian strewn field, and (2) a satisfactory explanation for the layered and irregular Muong Nong tektites. Dr Brian Mason (personal written communication) does not dispute the two enigmas (McCall 1997), but adds two further enigmas, which relate to the arguments set forth by Baker (1959, 1962), Gill (1970) and Lovering *et al.* (1972), which were supported by Chalmers *et al.* (1976), vigorously disputed by Glass (1978), restated again by Chalmers *et al.* (1979) and finally countered by Glass (1979) in a reply. Mason wrote in his communication to the author

"...there are two enigmas:

1) the age paradox: most australite investigators, myself included, believe their terrestrial age is around 10 000 years (5 000).

2) Why has no one found micrometeorites on land in Australia (many thousands of soil samples have been examined)?"

(Mason, personal communication).

This retention of the "age paradox" is surprising because, after an exhaustive study of the literature, McCall (1997) had come to assume rightly or wrongly that it was no longer tenable, and that most workers on tektites accepted this. It seems that, 20 years later, there is a case for reconsidering the problem, which provides an interesting illustration of the philosophy involved in a scientific controversy in which there is an apparently irresolvable conflict of evidence. New indirect evidence bearing on the controversy has accrued in the intervening years, and lately some new direct evidence has come to light in Australia.

The fundamental concern of the age paradox was the fact that the apparent stratigraphic ages of australites (that is the age of the formations in or on which they are found) are nowhere near as great as the radiometric ages (K-Ar, Ar-Ar, fission track) determined for them and which are widely taken to give the age of fall to Earth (such values actually relate to the solidification of the tektite glass, but in terms of the Geological Time Scale the separation of this from the time of fall to Earth is infinitessimal). Whereas stratigraphic ages range from about 20 000 years, down to 6 000 years and even younger, the radiometric age determined on tektites throughout the entire Australasian strewn field is widely taken to be 0.77 million years (Izett & Obradovich 1992). This age is also widely accepted for microtektites from the ocean adjacent to Australia, because it is established by their presence just prior to the the Brunhes-Matuyama reversal boundary (Glass & Wu 1993), which is placed at 0.78-0.79 million years ago, on the basis of Ar/Ar dating of extrusive rocks which bracket it (Fudali 1993).

It should be noted here that Bottomley & Koeberl (1999) have recently published results of research that indicates that there may be two tektite strewn fields, an Australasian one and another smaller Australian one of greater age (about 10 million years). Interestingly, most of the high soda australites which have yielded this higher radiometric age come from the NW quarter of South Australia, not very far from the Lake Torrens area, where the very young australites have been postulated by Lovering *et al.* (1972). This new discovery means that there is now an absolute "age paradox" of a different nature, complicating the picture, but this development has no bearing on the problem discussed in this text.

Stratigraphic age

Australia

Australia lies at the southern (distal to source) end of the largest known tektite strewn field (the Australasian strewn field; Fig 1). The evidence of the stratigraphic age of australites in Victoria and Western Australia is not precise (Baker 1959; Barnes 1963). At Port Campbell, Victoria, tektites are definitely younger than the Miocene limestones, but "do not occur in the nearby post-Pliocene dune limestone of the district, and are therefore post-Pliocene" (Baker 1959). This poses the question, what is the exact age of the dune limestone? It also poses the question whether non-occurrence in a formation proves that the date of fall was younger than that formation. Processes of accumulation in terrestrial sediments are very complex and not every formation deposited after the arrival of a tektite shower can be expected to contain them in sufficient quantity to be detected; some may not contain them at all. The tektites were said by Baker (1959) to occur at Port Campbell partially buried in post-Miocene superficial clays and surface soil, and he added "their occurrence in surface soils indicates a still younger geological age for some specimens", but this does not seem to have any bearing on the age of fall; it only indicates reworking from older formations.

Fudali (1993) re-examined the evidence from Port Campbell, as well as sites nearby at Stanhope Bay and inland. The field evidence differs from that given by Baker (1959); he relates the tektite concentration to a sandstone layer with buckshot gravel, whereas Baker (1959) described them as buried in superficial clays and surface soils. Nevertheless, Fudali (1993) made some important observations.

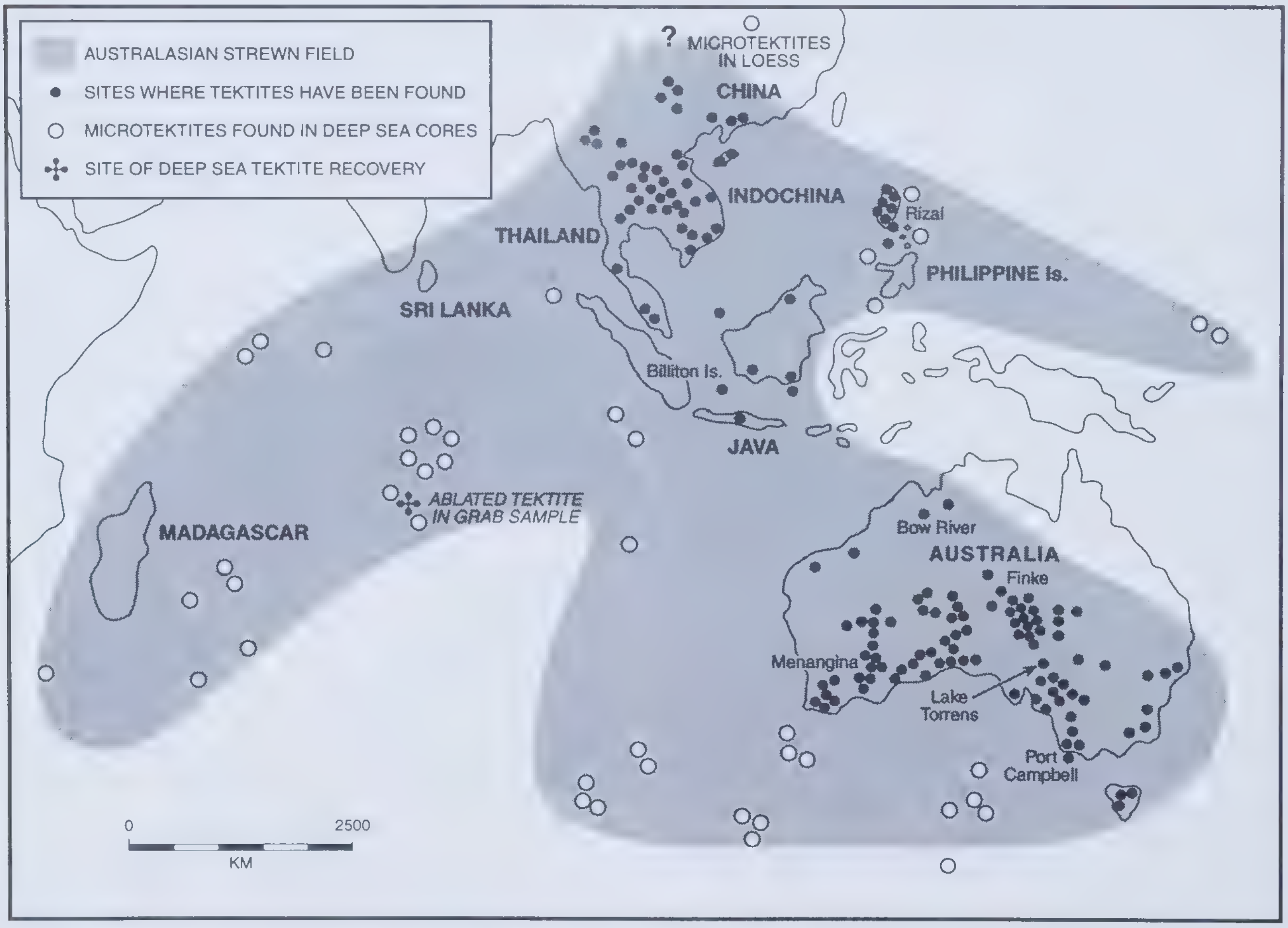
AUSTRALASIAN STREWN FIELD
● SITES WHERE TEKTITES HAVE BEEN FOUND
○ MICROTEKTITES FOUND IN DEEP SEA CORES
SITE OF DEEP SEA TEKTITE RECOVERY
? MICROTEKTITES IN LOESS
CHINA
INDOCHINA
Rizal
PHILIPPINE Is.
THAILAND
SRI LANKA
Billiton Is.
JAVA
ABLATED TEKTITE IN GRAB SAMPLE
MADAGASCAR
Bow River
AUSTRALIA
Finke
Menangina
Lake Torrens
Port Campbell
0
2500
KM

Figure 1. The Australasian strewn field (slightly modified from the figure presented in McCall 1997).

1) At Stanhope Bay, the tektites were described by Gill (1970) as resting on recent sand-dunes, where they had either fallen directly or been carried by Aborigines. Fudali (1993) observed that they are all water-worn and thus must have undergone natural transport to where they now were found; they could not, therefore, be at the site of fall.

2) The tektites recovered from a 256 m^2 patch of ground near Port Campbell by archeological-type digging (excavating down to the 'hardpan') were all fragments, and mostly derived from flanges of ablated tektites; they could not in any way be fitted together nor make up whole tektites by such assemblage, and the conclusion of Fudali (1993) was that they were sorted by size or shape, during transport.

3) A few tektites from Port Campbell were found embedded in the aeolian sandstone beneath the tektite rich layer. Fudali (1993) demonstrated that they had not fallen into cracks from above, as had been previously suggested, but were actually within the rock. This aeolianite has not been accurately dated, but is generally regarded as Pleistocene. It is not absolutely clear from Fudali's account which rock this is, but it seems that the "dune limestone' of Baker (1959) is the 'sandstone aeolianite' of Fudali (1993).

Fudali's (1993) succinct conclusion is that the proposed 5 000 yr (Baker 1959) to 15 000 yr (Gill 1970) maximum age of fall is demonstrably incorrect and that the australites are found in a formation older than those described by the above authors. Fudali (1993) also used cosmogenic radionuclide data to support this contention.

We will return to the almost pristine preservation of flanged forms at Port Campbell later, and even more recent investigations there. Both Baker's (1959) assertion that the tektites must have fallen no more than *ca* 5 000 years ago and Gill's (1970) figure of 15 000 yr, based on a radiocarbon date on the middle of the 'hardpan', do not seem to rely on anything but the excellent preservation of some of the australites, which is not disputed. Though Fudali (1993) regarded these Port Campbell australites as "unique among all known australites... most being unmarked by mechanical abrasion and showing only very minor chemical etching", equally perfect forms have been recorded by the late W H Cleverly (1988, 1994) from Gindalbie and Menangina Pastoral Stations (Western Australia) and Finke (Northern Territory). Port Campbell australites are remarkable, but by no means unique.

In Western Australia, tektites are mainly recovered from the surface of saline playa lakes. They tend to resist the corrosive effect of the salt, but are commonly mechanically abraded, although excellent flanged forms comprise a minority of such recoveries. These lake surfaces are present-day saline claypan surfaces and, whereas tektites are found on and in superficial deposits widely over the State, there has been no systematic study of derivation of tektites from within dated sedimentary formations and indeed such a study might be tediously difficult (given the abundance of laterites, silcretes *etc*), though any evidence of tektite recoveries from within such sediments would be critical to this discussion. Perhaps the best chance of finding tektites in older, datable (Pleistocene) sediments associated with these lakes lies in the thick sections of unconsolidated sediments beneath the surficial clays of the large lakes between Kalgoorlie and Norseman, but the chance of finding a tektite within a small diameter core recovery is very small, and the Pleistocene representation is reportedly thin. Microtektites could, however, conceivably be found in cores of these sediments, if they have not been dissolved by the saline waters.

Recently, however, discoveries of tektites within sediments have been described from the Bow River area of the extreme north of Western Australia (Fudali *et al.* 1991; Fudali 1993). Tektites are rarely found on the surface here; the much higher rainfall than in the remainder of the State apparently washes them into sedimentary deposits. These finds are in diamondiferous gravels and Fudali (1993) cited ^{3}He isotope determinations of cosmic-ray exposure age for the diamonds to indicate an age of at least 250 000 years for these deposits. The method used has some uncertainties and cannot be used to fix a precise age for the diamondiferous gravels, but it does seem to preclude the very young ages for the tektites suggested by Baker (1959, 1962), Gill (1970) and Lovering *et al.* (1972).

Only in the Lake Torrens area of South Australia has detailed sedimentological evidence of tektite recoveries and their absence from dated sediments been gathered (Lovering *et al.* 1972) and this work really provides the crux of the argument for a fall age of no more than 24 000-16 000 years. Australites are recovered from interdune corridors, floored by clayey sand dated at *ca* 6 000 yr (Holocene), also from modern sand dunes, and the Motpena palaeosol (*ca* 12 000 years old), Lovering *et al.* 1972 considered the relict seif dunes of the Lake Torrens formation (24 000-16 000 yr) to be the "ultimate source" of the tektites Good flanged button forms are illustrated, but the surfaces are quite pitted and they have clearly suffered some terrestrial degradation.

The basic stratigraphic relationships as far as they are known were known at Port Campbell, Lake Torrens and Western Australia, when the "age paradox" was proposed, are summarised in Fig 2. At Port Campbell, tektites are found in recent soils and superficial clays, buckshot gravel and, rarely, in the aeolianite below. In the Lake Torrens area, they are found in or on three ages of formation, a modern dune sand and an older palaeosol, as well as a clayey Holocene sand in the corridors, and are believed to have an "ultimate source" in the older Torrens relict seif dunes (of Wisconsin age, no more than 24 000 yr). There is clear evidence that they occur in deposits of several ages. In the southern part of Western Australia, they are found on active saline clay pan lakes and around their fringes, also in or on superficial deposits away from the lakes. They have clearly been washed in onto the lake surfaces of clay or salt, but there is little or no evidence as to the nature of the older source formations from which they have come. Tektites are also found in diamondiferous gravels in the north of the State, and there is reason here to believe that the host sediments are at least 250 000 years old (but this discovery postdated the original controversy by more than a decade).

Only for the Lake Torrens area, other than reliance on the good state of preservation of flanged australites, have

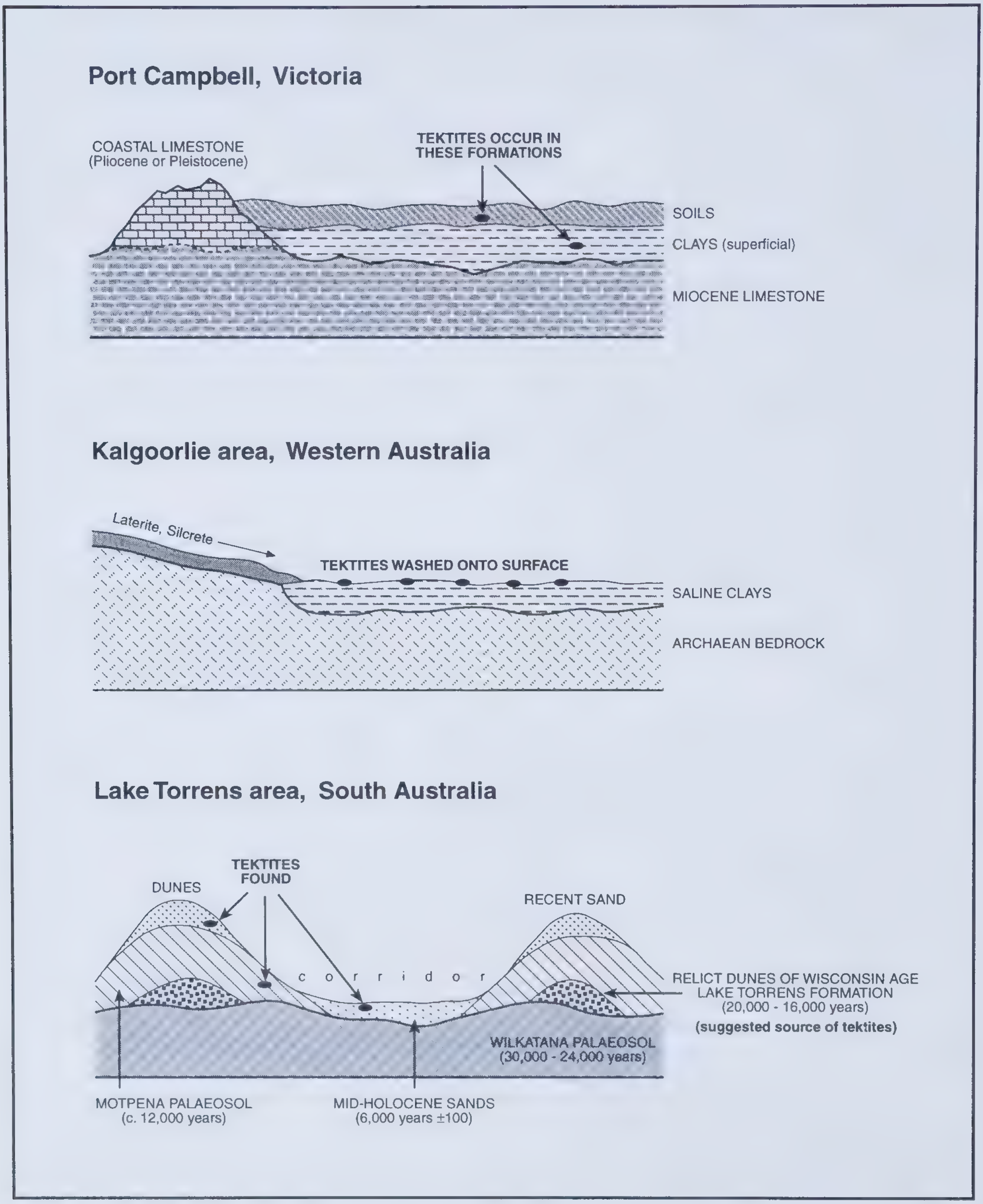

Figure 2. Schematic drawing illustrating the essential relationships at Port Campbell, Victoria (following Baker 1962), Lake Torrens, South Australia (following Lovering *et al.* 1971) and in Western Australia (Kalgoorlie region).

arguments been advanced for the tektites having not been transported any distance and being recovered close to where they fell. Besides citing the state of preservation of the australites at Motpena and Myrtle Springs, it was noted by Chalmers *et al.* (1979) that the nearest possible older source formation is 25 km northward of the find sites and transport by vigorous streamfloods thence could not, they believed, have been undergone by the delicate forms preserved. In addition, it was argued that the Lake Torrens region is a tectonic depression which has been sinking throughout Holocene times, so a 770 000 year old horizon will be deeply buried and inaccessible to erosion. Localisation of specific gravity groups and geochemical groups to different find sites also was taken to indicate that individual find sites correspond to fall sites closely, otherwise such groupings would have been lost by transport and reworking.

As in the case of Western Australia, new evidence has emerged regarding the Lake Torrens occurrences. Shoemaker & Shoemaker (1997) looked again at the dunes there and observed an invariable association of australites with stones of like dimensions, the latter vastly outnumbering the tektites (they suggested a proportion of 10 000 stones to one australite). Transport by Aborigines was suggested to explain the movement of some of the stones and the tektites onto the dunes, but the high ratio observed suggests that some natural agency may have been involved rather than a human agency. A possible agent is the very common dust-devil whirl-winds (or "Cock-eyed Bobs") that are common in the hot, dry interior of Australia. Might innumerable repetions of such miniature tornados, over long periods, be capable of taking up into the air and redepositing stones and tektites?

No recovery of microtektites on land in Australia

The author does not find the absence of recovery of microtektites on land in Australia to be a very strong argument for a young age of fall; in deep sea cores concentrations of microtektites are found in sediments of the same age as the radiometric age of the tektites in the Australasian strewn field. Such fine material might be found concentrated in sediments ***of the same age*** on land; but, the author is not sure that any search has been made of sections through sediments of that age in Australia. However, if the older radiometrically-determined fall age is correct for the Australasian strewn field, then it is extremely unlikely that they could be found in superficial soils, as Glass (1979) concludes in his reply. On land, the dissolution rate of tektite glass is second order of magnitude larger than in the ocean; it has been shown that on land the dissolution rate of tektite glass is a much higher than in seawater, where magnesium appears to act as a buffer (C Koeberl, Universität Wien, personal communication). The absence of microtektites from such deposits appears to be in no way inconsistent with the 0.77 Ma radiometrically-derived fall date. Mason's second enigma above does not appear to be valid.

In addition, Glass & Wu (1992), from a study of deep-sea cores, showed that there was no microtektite productivity event in the ocean around Australia *ca* 20 000 years ago, or less.

Evidence from other strewn fields

North American strewn field

The age paradox is not peculiar to Australia. It was for a long time also suggested in the much older North American Strewn Field (Fig 3), where Texas bediasites are found in gravels above and much younger than late

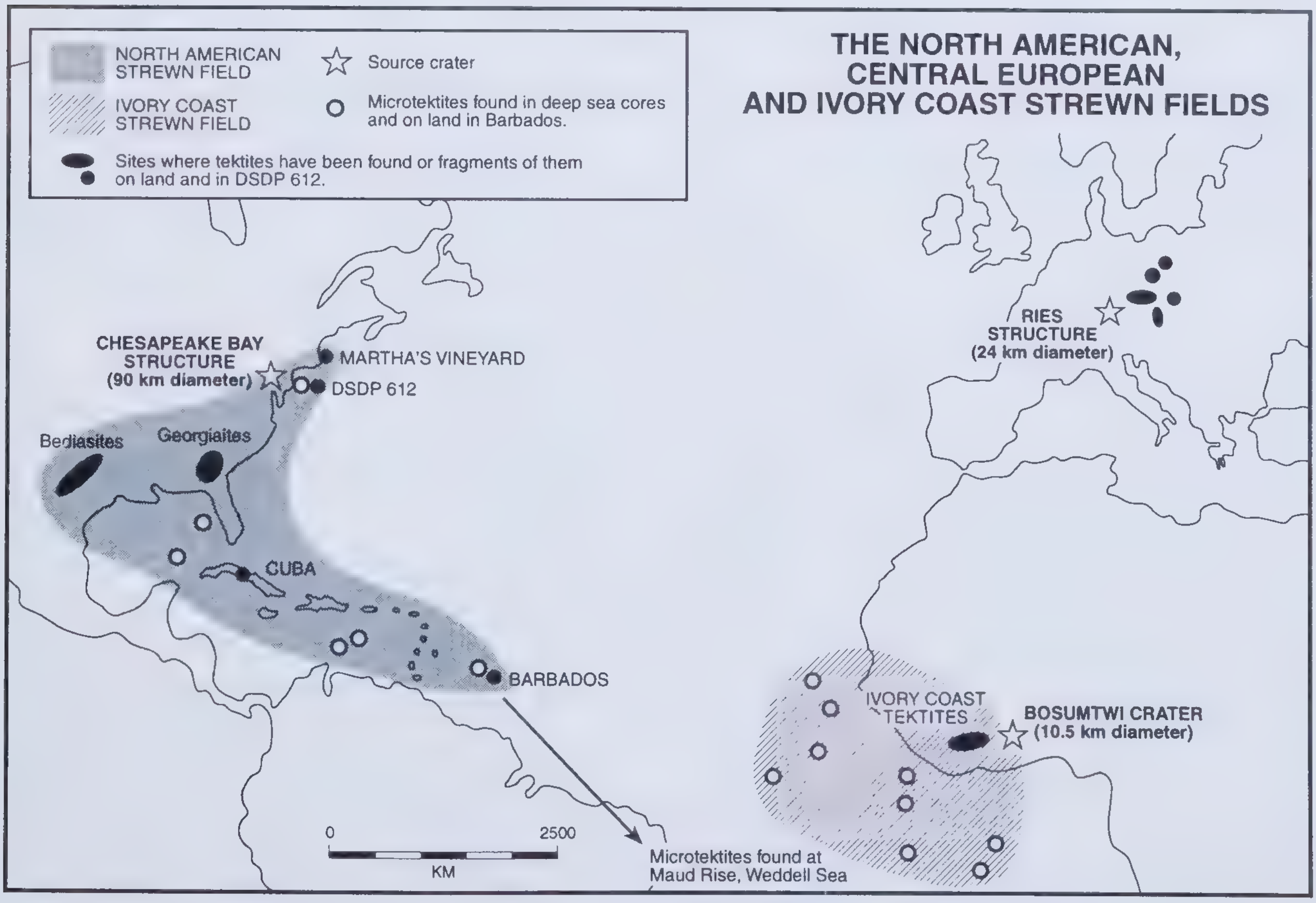
NORTH AMERICAN STREWN FIELD
IVORY COAST STREWN FIELD
Source crater
Microtektites found in deep sea cores and on land in Barbados.
Sites where tektites have been found or fragments of them on land and in DSDP 612.
THE NORTH AMERICAN, CENTRAL EUROPEAN AND IVORY COAST STREWN FIELDS
CHESAPEAKE BAY STRUCTURE (90 km diameter)
MARTHA'S VINEYARD
DSDP 612
Bediasites
Georgiaites
CUBA
BARBADOS
RIES STRUCTURE (24 km diameter)
IVORY COAST TEKTITES
BOSUMTWI CRATER (10.5 km diameter)
0
2500
KM
Microtektites found at Maud Rise, Weddell Sea

Figure 3. The North American, Ivory Coast and Central European Strewn Fields (slightly modified from McCall 1997).

Eocene rocks, and georgiaites are found in gravels above Miocene rocks, that the stratigraphic age was much less than the radiometric age; 34-35 Ma, equivalent to the very top of the Eocene. However this paradox disappeared with the discovery of tektite fragments and microtektites together in core at DSDP 612 of the New Jersey Coast (Glass 1989) and in sediments on land at Barbados (Sanfilippo *et al.* 1985; Koeberl & Glass 1988). In both localities the stratigraphic age of the containing sediments and the radiometric age of the North American tektites almost exactly matched. A 90 km diameter structure in Chesapeake Bay was also found to be of the same age, *ca* 35.5 Ma, and deemed to be the source of the strewn field (Koeberl *et al.* 1996).

There are a number of further points to make about this strewn field. The tektites, inevitably much corroded and abraded because of their greater age on Earth than those of the Australasian strewn field, only occur in certain formations where they have presumably been concentrated by some terrestrial agency. Many underlying, intervening, and younger formations within the limits of the strewn field must be devoid of them at least in such quantities as to be recognisable (this makes the point again that not finding them in a formation does not mean that the formation is older then the date of fall). Having said this, the time scale is quite different to the maximum possible scale from fall (as indicated by radiometric ages) to present day in Australia, being very much greater (34.5 as against 0.77 Ma), so these tektites have inevitably a much longer potential history of recycling. The evidence from the North American strewn field provides overwhelming support for the validity of radiometric ages as true indicators of the age of fall back to Earth. This strewn field also includes associations of microtektites recovered with fragments of tektites of the same composition (in DSDP 612 and at Barbados), which seems to dispel doubts expressed whether the microtektites are related to tektites in the Australasian strewn field. As far as the author knows, only a single aerodynamically ablated form has been described from the North American Strewn field.

Ivory Coast strewn field

Here (Fig 3) the tektites occur in superficial gold-bearing alluvial deposits close to the surface, and of quite recent age. The microtektites offshore from West Africa have a stratigraphical age constrained by the closeness of the microtektite bearing layer to the Jaramillo geomagnetic event (0.97 Ma; Glass *et al.* 1991); the tektites are believed to have fallen just after the beginning of the Jaramillo event. This, within the limits of error, is consistent with both the radiometric age of the tektites (1.07 Ma preferred age) and the age of the widely accepted source structure, the Bosumtwi crater in Ashanti (impact glass, fission track age 1.03 ± 11 Ma: Koeberl *et al.* 1997). Reliable radiometric ages cannot, unfortunately, be obtained for the microtektites, though two fission track determinations average to about the same figure (Koeberl *et al.* 1997). Here, as in Australia, the tektites occur in very recent but undated deposits and there is a time gap between the likely age of these and the radiometric age. Unfortunately, virtually no modern study has been made of the stratigraphy of the tektite bearing formation and only some 200 tektites have so far been recovered on land (McNamara & Bevan 1991). There are no aerodynamically-shaped flanged tektites.

Central European strewn field

The widely accepted source of this strewn field (Fig 3) is the Nördlinger Ries structure in southern Germany, dated by K/Ar and fission track methods at 15.1 ± 0.1 Ma (Staudacher *et al.* 1962) The tektites are found in gravels of the Helvetian stage (an obsolete term, modern equivalent Lower Vindobonian) of the Miocene of Moravia (Barnes 1963), which is quite consistent with a radiometric age of 15.1 ± 0.1 Ma also determined, on a moldavite tektite (Staudacher *et al.* 1982). Koeberl *et al.* (1988) reported moldavites from gravels of probable Miocene age in Austria, from Oligocene to Lower Miocene sediments in Bohemia and from Pliocene sediments in Moravia. They have clearly been reworked. There are no marine recoveries of microtektites from this strewn field, though they could well occur in the Baltic Sea (tektites have been recovered near Dresden). Microtektites have been recorded from 'molasse', Post-Alpine continental deposits, in Bavaria (Storzer & Gentner 1970), but these have been shown to be microscopic bodies of volcanic origin (Graup *et al.* 1981). There seems to be no age paradox in this strewn field. Again, there appears to be only a single record of an aerodynamically ablated form.

Inferences from outside the Australasian strewn field

The fact that all these three strewn fields do not now, since the recent discovery of the Chesapeake structure and the DSDP 612 and Barbados tektite occurrences, have any discrepancy beween radiometric age and age of the widely accepted source structures, and that in two out of three the greatest known stratigraphic age is compatible with radiometric age and that of the source structure, would seem to militate strongly for the radiometric age of tektites indeed indicating the age of fall *i.e* return to Earth. The difference in time between ejection from the source crater and fall to Earth again can have been no more than hours in the case of any of the known tektite strewn fields, as there is no evidence of complete Earth orbits. There is also conclusive evidence that tektites and microtektites are very closely related and together comprise three of the four strewn fields. Besides the evidence from Barbados and DSDP 612, the geographic patterns of distribution (Fig 3) also strongly support this. The new find of microtektites in ODP 689B on the Maud Rise of the Weddell Sea at 64° 31.009' S, 03° 05.996' E (Glass & Koeberl 1999), though extending the strewn field by a remarkable amount, still fits onto the extension of the Barbados ray of the pattern of non-homogeneity suggested by Koeberl (1989)

The following conclusions can be drawn concerning the Australasian strewn field

1) There should be source structure, once a crater, for the Australasian strewn field, since all the other three strewn fields have established source craters. A number of possible sites have been investigated or suggested (for example under the Mekong delta (Stauffer 1978), Tonle Sap, Cambodia (Hartung 1990), in Laos (Schnetzler & McHone 1996), offshore from Vietnam (Schnetzler *et al.* 1988) and somewhere in China (McCall 1997), without a positive result.
2) This crater should be *ca* 0.77 Ma old, consistent with the radiometric age of the tektites.

3) The radiometric age should indicate the age of fall to Earth of the tektites which is inseparable from the age of the source structure, being separated only by the very brief period of sub-orbital flight.
4) The suggestion that microtektites are not related to the same event as the Australasian tektites seems difficult if not impossible to maintain in the light of the North American and Ivory Coast evidence, similarity of geochemical composition and isotopic signatures (for example, Glass 1990; Shaw & Wasserburg 1982), not to speak of the geographical patterns and age relations in all three strewn fields other than the Australasian (and indeed the geographical pattern in the Australasian strewn field itself and the recovery of an ablated tektite from the middle of the Indian Ocean amidst a cluster of microtektite recoveries (Glass *et al.* 1996).
5) Lack of recovery of tektites from a stratigraphic formation does not necessarily mean that it is older than the arrival of the tektites.
6) Tektites have been reworked by geological processes in all the other three fields and there is evidence for recent reworking in Australia.
7) The lack of microtektites in recent soils is not inconsistent with the radiometric age being the age of fall to Earth.
8) There is some evidence from the Bow River in the north of Western Australia of tektites in a formation of much older stratigraphic age than that suggested from Lake Torrens, although the method used cannot precisely date the tektite-bearing gravels.
9) The evidence of Glass & Wu (1992) that no microtektite productivity occurred around Australia at 20 000 years or less strongly indicates that there was no late Pleistocene tektite event in Australia.

Having said all this, the study of Lovering *et al.* (1972) is extremely difficult to fault, and if the conclusion of these authors and Mason (personal communication) are incorrect, then we have to accept that extremely well preserved flanged button ablated tektites can undergo several cycles of geological redistribution over a period of three quarters of a million years, while others have become abraded, fragmented and even may have lost all traces of ablation, and that somehow, some have managed to escape such degradation and preserve the delicate flange. The Port Campbell australites are the best preserved as a group, yet they, like the equally well-preserved examples from Lake Torrens and Western and Central Australia, were recovered alongside degraded, fragmented and manifestly transported forms. Some flanged buttons from Port Campbell, Lake Torrens and Western and Central Australia are illustrated (Fig 4). An example of partial preservation of the flange, with the scar where the remainder detached; a 'core' in which only the circumferential detachment scar is left; and a highly degraded example, all three from Finke, Northern Territory (Cleverly 1988), are illustrated in Fig 5. The complexities of behaviour of australites in ablating flight were well illustrated by Cleverly (1987); complete or partial parting of the stress shell commonly occurred, preservation of stress shell and flange being exceptional, and after fall to Earth, there was a wide disparity in the activity of agents of geological degradation on australites, even from the same site (in this case Ravensthorpe, Western Australia). We have to accept that the almost pristine ablated forms illustrated in Fig 4 have somehow survived for 0.77 Ma and escaped the degradation that is evident for the last two illustrated in Fig 5, incredible though this may be.

The author believes that one has to accept, after considering all the weighty indirect evidence listed above, that some flanged button australites were able to pass through several cycles of geologic redistribution over a period of 0.77 Ma without severe modification by erosive agencies. Those that survived in Victoria, South Australia, Western Australia and the Northern Territory were probably a minority; this is certainly true of Western Australia. The flanged form must, if this is true, be more resistent to abrasive degradation than we have hitherto believed.

We also have to accept that in Victoria, South Australia, Western Australia and Central Australia, there must have been older, tektite-bearing geological formations, of which we have no knowledge (despite the evidence advanced against this from Lake Torrens advanced by Chalmers *et al.* 1979). We will almost certainly never know anything of the "dark ages", the intervening stages of redistribution and lodgement in older formations than those from which the tektites are recovered, unless, by chance, a concentration of tektites is found in such an older formation (as may have occurred at the Bow River). The geological record is a very imperfect data-base and has a bias towards what we can now see at the surface, despite the contribution of drill cores. Tektites may have been very dispersed in the older formations and undergone concentration in the younger recovery formations. We will probably never know how these ablated forms came to be preserved, though some form of protection such as entrapment in clay over much of their history could be invoked. A clue might be found in the fact that some of Baker's Port Campbell collection reportedly comes from a clay deposit.

If we accept that radiometric age equals age of fall to Earth, then we have to discount the evidence of specific gravity and chemical variation advanced by Chalmers *et al.* (1979) to show that the site of recovery is very close to the site of fall, a major step but one that is unavoidable. The preference for this solution owes something to "Occam's razor, that entities are not to be multiplied without necessity." The author believes that this must be the correct solution, remarkable though it is, and it is not one of an age paradox requiring two distinct arrival events; the requirement to explain the apparent age paradox lies in accepting that these apparently fragile objects (ablated flanged tektites) have survived on Earth for a period of 0.77 Ma, and that there must have been stages in their passage from fall to their present find sites of which we have no evidence or knowledge. Otherwise, if we accept the alternative solution, then we are left with a pattern of microtektites recovered from the ocean surrounding Australia, coincidentally of the same stratigraphic age as the derived radiometric age of the australites recovered from the continent, but with no equivalent tektites on the continent. Surely, this is a highly improbable coincidence? We are also left with the

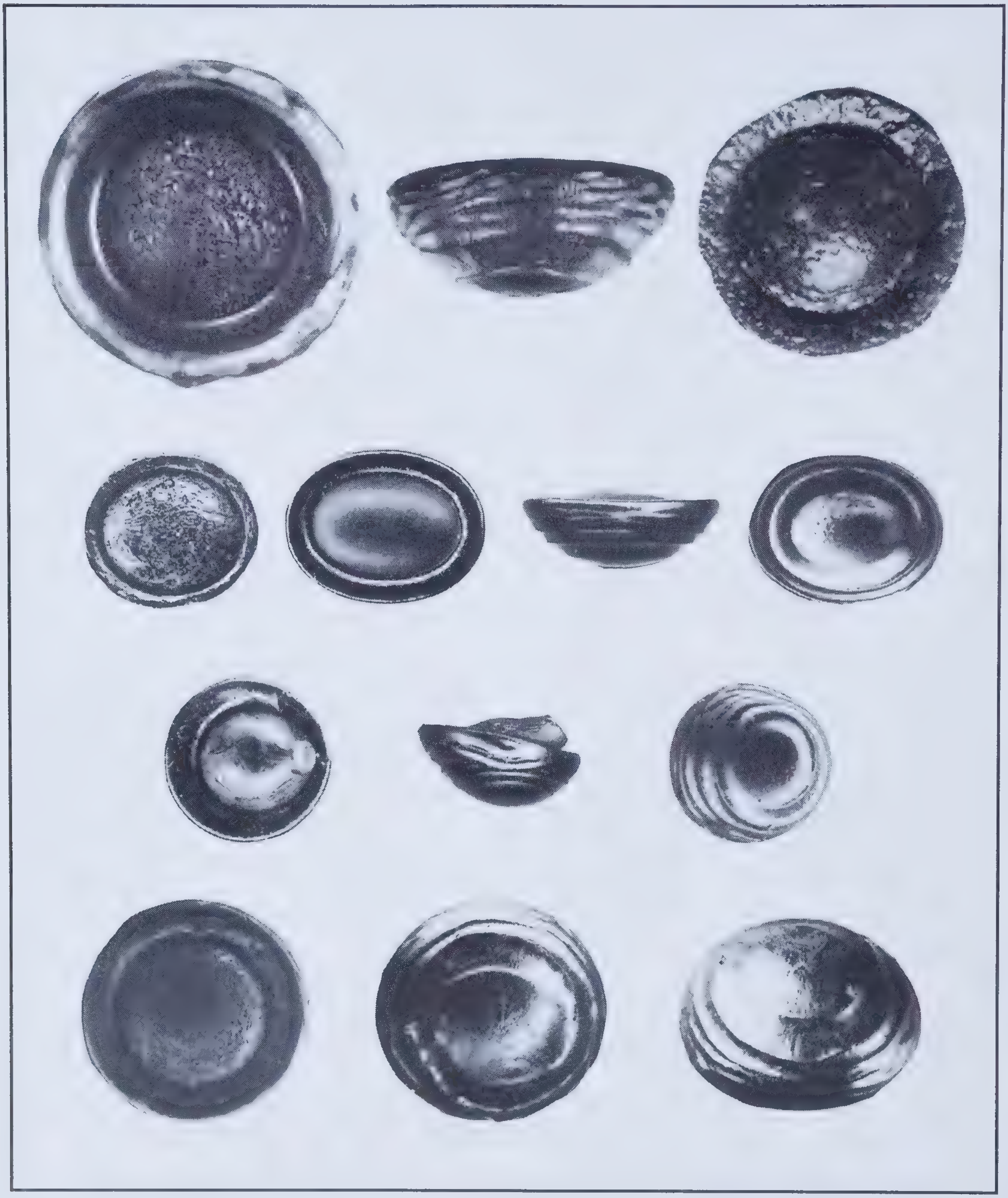

Figure 4. Examples of remarkable preservation of flanged button ablated australites. **Top row**: from Port Campbell, posterior and side view (Photographs: Baker 1963, magnification x 2.4): from the Myrtle Springs interdune corridors (Photograph: Lovering *et al.* 1972, maximum dimension 10 mm). **Second and third row**: from Gindalbie and Menangina Stations, Western Australia (Photographs: WH Cleverly 1994, maximum dimensions about 20 mm). **Bottom row**: from Finke, Northern Territory (photographs: WH Cleverly 1988 maximum dimensions about 20 mm)

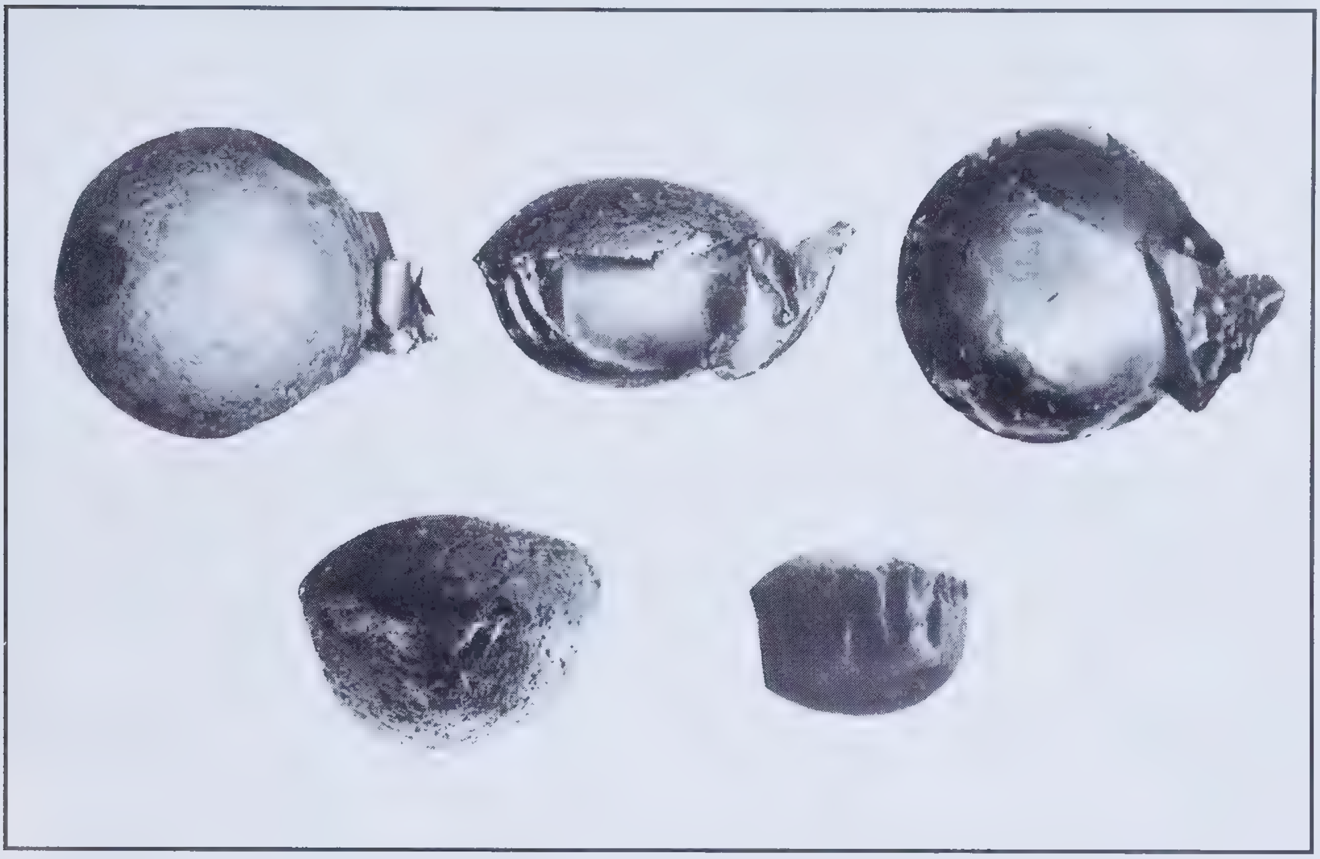

Figure 5. Three tektites from the vicinity of Finke, Northern Territory, Australia: (Photographs: WH Cleverly 1988). **Top row**: with partial flange preserved, showing the equatorial flaked zone where it has been partly lost, three views (maximum dimension 35.6 mm). **Bottom row**, right: without any flange, but showing the equatorial flaked zone where the flange has separated (maximum dimension 35.3 mm): left; without any flange, much more degraded by terrestrial transport and abrasion (maximum dimension 17.5.mm)

radiometric age being the age of ejection from impact structures and return to Earth in the three other strewn fields, but not in Australia!

An additional question arises; if australites could survive for 0.77 Ma on Earth as flanged buttons, why are no ablated forms found among the south-east Asian recoveries? Though the climate in south-east Asia is quite different to that of Australia and would have favoured quicker degradation, a few ablated forms surely should have survived among the thousands of tektites from Indochina? The probable answer to this question, considering that the furthest north that ablated tektites have been described from the Australasian strewn field is Java and Flores, Negros Island, Philippines, and the Central Indian Ocean, is that, although the source is not known, the northern recoveries are proximal to the source, and their trajectories did not involve exit from and re-entry to the atmosphere. Thus, only primary splash forms have been recorded.

Shoemaker & Uhlherr (1999) add significantly to the Port Campbell picture in showing that australites, including complete aerodynamically ablated forms, occur in ferruginous sandstone clasts within the late Pleistocene-Holocene Sturgess Sand formation, reworked from the underlying Pliocene-Pleistocene Hanson Plain Sand (and weakly cemented sandstone), in which australites are also found in channel deposits. They concluded that as australites occur in strata older than the late Pleistocene-Holocene Sturgess Sand, there is no longer any conflict in the Port Campbell area between the apparent stratigraphic age of the tektites and the middle Pleistocene ages obtained by chronometric methods. These authors also noted the presence of australites together with mollusc shells in aboriginal middens, evidence that Aborigines have transported tektites.

Koeberl (1994) observed "The hydra of the so-called age paradox occasionally rears its heads and needs to be addressed at least briefly......" Surely, now, we can say that the "hydra" has at last been given the coup-de-grace?

Acknowledgments The author acknowledges the assistance of AWR Bevan, BP Glass, C Koeberl and an unnamed referee all of whom who supplied several obscure and recent additional references which have greatly improved the original text. He is also indebted to the late WH Cleverly, who passed to him a wealth of illustrations of australites shortly before his death. B Mason inspired this review and again supplied a number of references.

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Biosystematics of two new species of unusually coloured Australian mygalomorph spiders, *Arbanitis* (Araneae: Idiopidae), from south-western Australia

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Abstract

Two new unusual mygalomorph species, *Arbanitis mcmillani* and *Arbanitis ballidu*, are described from south-western Australia. In both species the integument of the carapace is white with an enamel-like sheen. The white colouring is derived presumably from pigment (possibly guanine) deposits in the cuticle. It is postulated that this unusual colour pattern of white contrasting with dark brown appendages and abdomen may render the spiders cryptic against a background habitat of litter on white or yellow sand.

Introduction

The trapdoor spider genus *Arbanitis* Koch as currently defined (Main 1985a; Raven 1985) is distributed widely in Western Australia south of the Tropic of Capricorn, and in eastern Australia from northern Queensland to Victoria and Tasmania, but appears to be absent from the Northern Territory and South Australia (Main 1985a,b, 1995). The genus also occurs in New Zealand (Main 1985b). There are currently 11 species of *Arbanitis* recognized as valid in Australia (Main 1985a,b, 1995) including three from Western Australia (Main 1985b). However it is apparent from collections that there are many more unnamed species on both sides of the continent.

Use of the name *Arbanitis* has always been problematical due to the apparent loss of the holotype of the type species *A. longipes* (Koch). Recently a specimen that is believed to be Koch's type (RJ Raven, Queensland Museum, personal communication) has been found in the Zoologisches Museum of the University of Hamburg. This may require nomenclatural changes that may later necessitate transference of the two species described here to the next available generic name *Euoplos* Rainbow.

Species of *Arbanitis*, as defined at present, all build doors to their burrows and usually occur in damp, shaded situations. Even those that occur in semi-arid regions are confined to seasonally damp microhabitats. Doors are usually thick, plug-like structures which fit tightly into the rim of the burrow. While most species occur in heavy clay or loamy soils, a few are known from sandy habitats.

Spiders of the genus *Arbanitis* are usually tan to reddish brown, or black, with glabrous carapace and legs; the abdomen may have dorsal paler banding; the legs are generally heavily spined. Males have long legs and are sometimes very dark, or black, in colour. This paper describes two new species of *Arbanitis* in which the male has an unusual colouring of the carapace, white with an enamel-like sheen. It is possible that this seemingly stark, contrasting colour pattern of shiny white carapace and dark brown abdomen and appendages is disruptive and renders the spiders inconspicuous on white or yellowish sand amongst litter beneath shrubby vegetation.

Systematics

Abbreviations

ALE, anterior lateral eyes; **AME**, anterior median eyes; **PLE**, posterior lateral eyes; **PME**, posterior median eyes. **v**, ventral; **d**, dorsal; **p**, prolateral; **r**, retrolateral (in reference to paired tarsal claws and position of leg spines). **WAM**, Western Australian Museum.

Measurements are in millimetres.

Arbanitis mcmillani sp nov

(Figures 1, 2 A-N; Table 1)

Holotype: Male, Eneabba (sand mine rehabilitation site 7 of RGC Eneabba) now Westralian Sands Eneabba), Western Australia (29° 49′ S, 115° 16′ E), live spider collected by R P McMillan, April 1992 (WAM 92/517).

Paratype: Male, as for holotype (sand mine control site 8), collected by R P McMillan and P West, 8 August 1998 (WAM 98/1590).

Diagnosis (male). Medium sized, generally dark reddish brown to black, femora of all legs and patellae III and IV dark, other leg segments pale, carapace white,

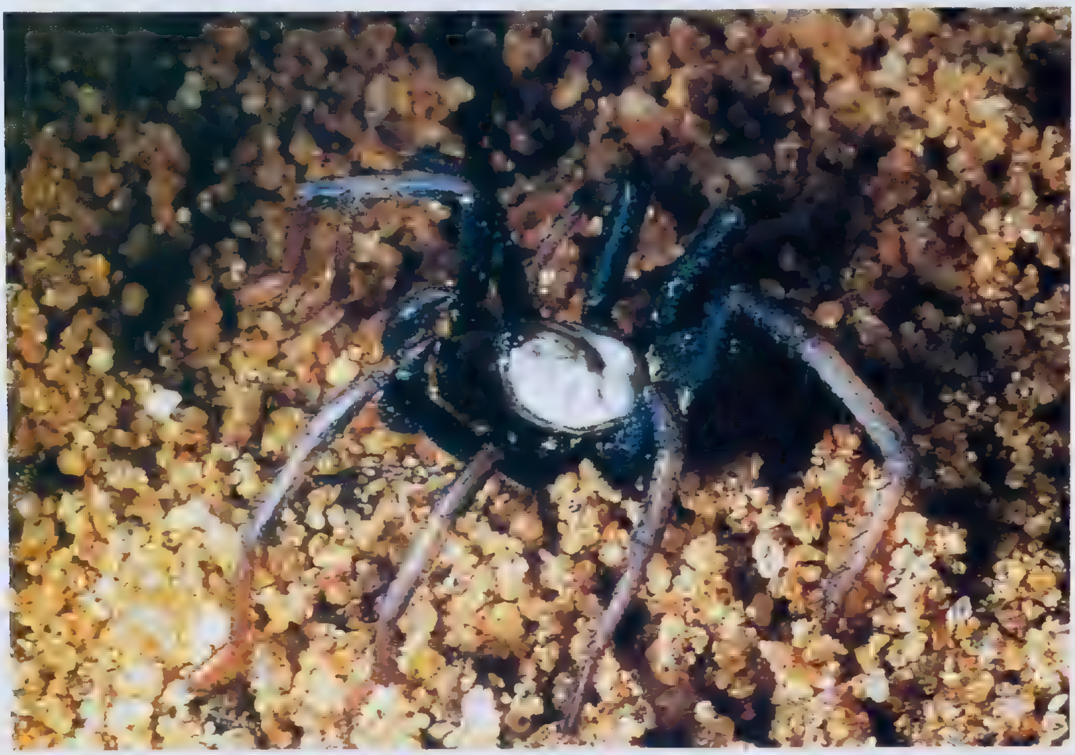

Figure 1. *Arbanitis mcmillani* sp nov, male (holotype) in life. (Photo R P McMillan).

glabrous, with an enamel-like sheen, and with black, rod-like spines. Labium with a few elongate cuspules. Palpal tibia with pronounced process with many stout spines (at least 30); embolus with prong-like tip; tibia I without apophysis but with a proventral comb of three spines. Tarsi I - III without spines.

Female unknown.

Description

Male (holotype). *Colour* Carapace white, with an enamel-like sheen; bearing black, rod-like, terminally truncate spines and bristles of uniform thickness except slightly thinner at base; ocular area black. Femora of legs and patellae III and IV dark brown, other leg segments pale, tarsi reddish. Sternum and palpal coxae reddish, chelicerae dark reddish-brown. Abdomen (slightly shrivelled) black dorsally, ventrally dark except lung covers and anterior to epigastric furrow yellow. *Carapace* length 5.2 mm, width 4.5 mm; radial depressions. *Fovea* pit-like, irregular outline, almost straight with deep, bowl-like posterior depression. Eyes on a dark mound, group width 1.1 mm, length 0.6 mm; anterior row procurved. Eye diameters; ALE 0.3, AME 0.25 (left,) 0.2 (right), PLE 0.3, PME 0.2. *Chelicerae* with asymmetrical teeth numbers, (right) promargin 4 large, 3 small teeth , 2 small basal intermediate, retromargin 7 large, (left) promargin 5 large, retromargin 4 large and about 5 small, granule-like in irregular pattern. *Sternum* length 2.9 mm, posterior sigilla oblong with right sigilla damaged and fragmented into 3 pieces (paratype normal, entire). *Labium* length 0.6 mm; with 3 finely pointed cuspules. *Legs* : *Scopula* complete on tarsi I and II. *Trichobothria* all long and hair-like, about 15 on tarsi I, none baton-like or clavate. Paired *tarsal claws* long and curved, I (long teeth), p 5, r 4, II (long teeth), p 3 (basal tooth two pronged), r 3, III (relatively short teeth), p, r 3, IV (relatively short teeth), p, r 3. *Spines* Tarsi I - III without spines, tarsus IV with pv3, rv one thin bristle-like spine, metatarsi I and II without spines, metatarsi III and IV with scattered spines on all faces. Tibia I (Fig 2 H, I) ventrally with at least 7 spines plus a retro-apical spine and pro-ventral apical comb (in place of an apophysis) of 3 spines comprised of one stout spine, one long thin spine and a shorter middle spine. Femora all with a mid-dorsal line of about 8 spines. Many spines and bristles rod-like and blunt terminally, similar to carapace spines. *Palp* (Figs 2 J - N) with prominent ventral process, with over 30, stout, tooth-like spines, embolus broad, tapering terminally, tubular and with prong-like tip. Abdomen length 4.7 mm; evenly covered with thick, terminally blunt, slightly curved setae.

Table 1

Leg dimensions of holotype male of *Arbanitis mcmillani.*
Leg formula = length of leg divided by carapace length. Tibial index = width of patella x 100 divided by length of tibia + patella (Petrunkevitch 1942).

Leg formula: 4 / 4.21, 1 / 3.25, 2 / 3.00, 3 / 2.75

Legs	Fem	Pat	Ti	Mt	Ta	Total
I	5.3	2.4	3.6	3.6	2.0	16.9
II	4.8	2.2	3.3	3.4	2.0	15.7
III	4.2	1.8	3.0	3.3	2.0	14.3
IV	5.6	2.9	4.6	5.4	3.4	21.9
Palp	2.5	1.3	2.3	–	1.1	7.2

Width patella I at knee = 0.7. **Tibial index** = 11.7.
Width patella IV at knee = 0.8. **Tibial index** = 10.6.

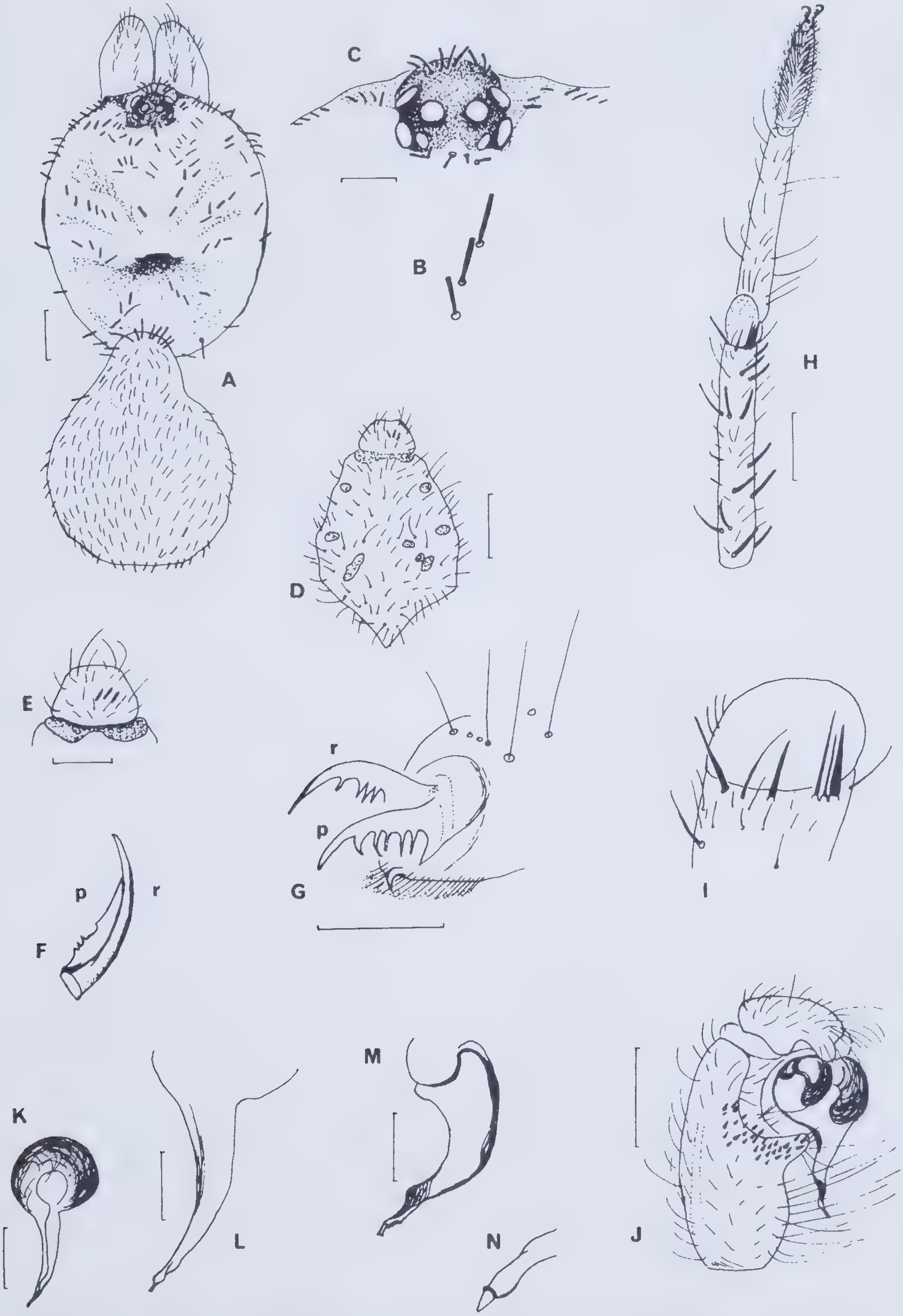

Figure 2. *Arbanitis mcmillani* sp nov, male (holotype). **A**, Dorsal view of spider, carapace and abdomen. **B**, Several spines of carapace enlarged. **C**, Eye group. **D**, Labium and sternum. **E**, Labium. **F**, Left fang, note keel and toothed promargin. **G**, Tarsal claws of right leg I, prolateral view (p, prolateral; r, retrolateral). **H**, Right leg I, tarsus, metatarsus and tibia ventral view. **I**, Apical ventral spines of right leg I showing proventral comb. **J** , Right palpal tarsus and tibia, retrolateral. **K**, **L**, Bulb and embolus, prolateral. **M**, Embolus, ventral. **N**, Embolus tip, ventral (enlargement of M view). Scale bars: **A**, **D**, **H**, **J** = 1.0 mm; **C**, **E**, **K** = 0.5 mm; **L**, **M** = 0.25 mm; **B**, **F**, **I**, **N**, not to scale.

Comments

The paratype is morphologically very similar to the holotype, with the same strikingly white, glabrous carapace and dark legs and abdomen. Carapace length/width, 4.9/4.3. The palp shows no distinctive variation and the tibia of the first leg similarly has a proventral, apical comb-like group of three (different sized) spines.

Habitat

Heath on white sand.

Etymology

The species is named after Peter McMillan, in gratitude for his generous and substantial donations of spider and insect collections to the WAM and in recognition of his wide entomological and natural history knowledge which always he has unstintingly shared.

Arbanitis ballidu sp nov

(Figures 3 A-F, Table 2)

Holotype: Male, Ballidu, Western Australia (30° 35' 28"S, 116° 45' 25" E), from wet pitfall trap, 24 May/16 September 1996, M S Harvey, B Y Main, J M Waldock (WAM 96/933).

Diagnosis (male). As for *A. macmillani*, carapace white, glabrous, with enamel-like sheen and scattered, black, truncate, rod-like spines, legs dark with tibia, metatarsi and tarsi paler. Labium without cuspules. Tibia I lacks apophysis, comb and heavy apical spines; a single pro-ventral, long tapering spine; tarsal claws of leg I with few teeth (fewer than *mcmillani*). Palpal tibia with slight process, few spines (no more than 20).

Female unknown.

Description

Male (holotype). *Colour* Carapace white, with black, teminally blunt spines. Appendages dark with pale terminal segments, abdomen black with small bare, white "wax" patches. *Abdomen* length 4.5 mm. *Carapace* length 4.4 mm, width 3.7 mm. Clypeus with four spines in a row and one large median spine (Fig 3A). *Eye group* width 0.9 mm, length 0.5 mm; anterior row straight. A group of about 14 rod-like spines on posterior of eye mound; four long clypeal spines, not rod-like. *Labium* length 0.4 mm, without cuspules. *Sternum* length 2.3 mm, width 2.0 mm.*Chelicerae*, asymmetrical teeth numbers, (right) promargin 5 large teeth, retromargin 6 teeth of uneven sizes, (left) promargin 5 large teeth, retromargin 5 and 2 tiny intermediate teeth. *Legs* *Scopula* dense on tarsi I and II, none on III and IV, none on metatarsi.

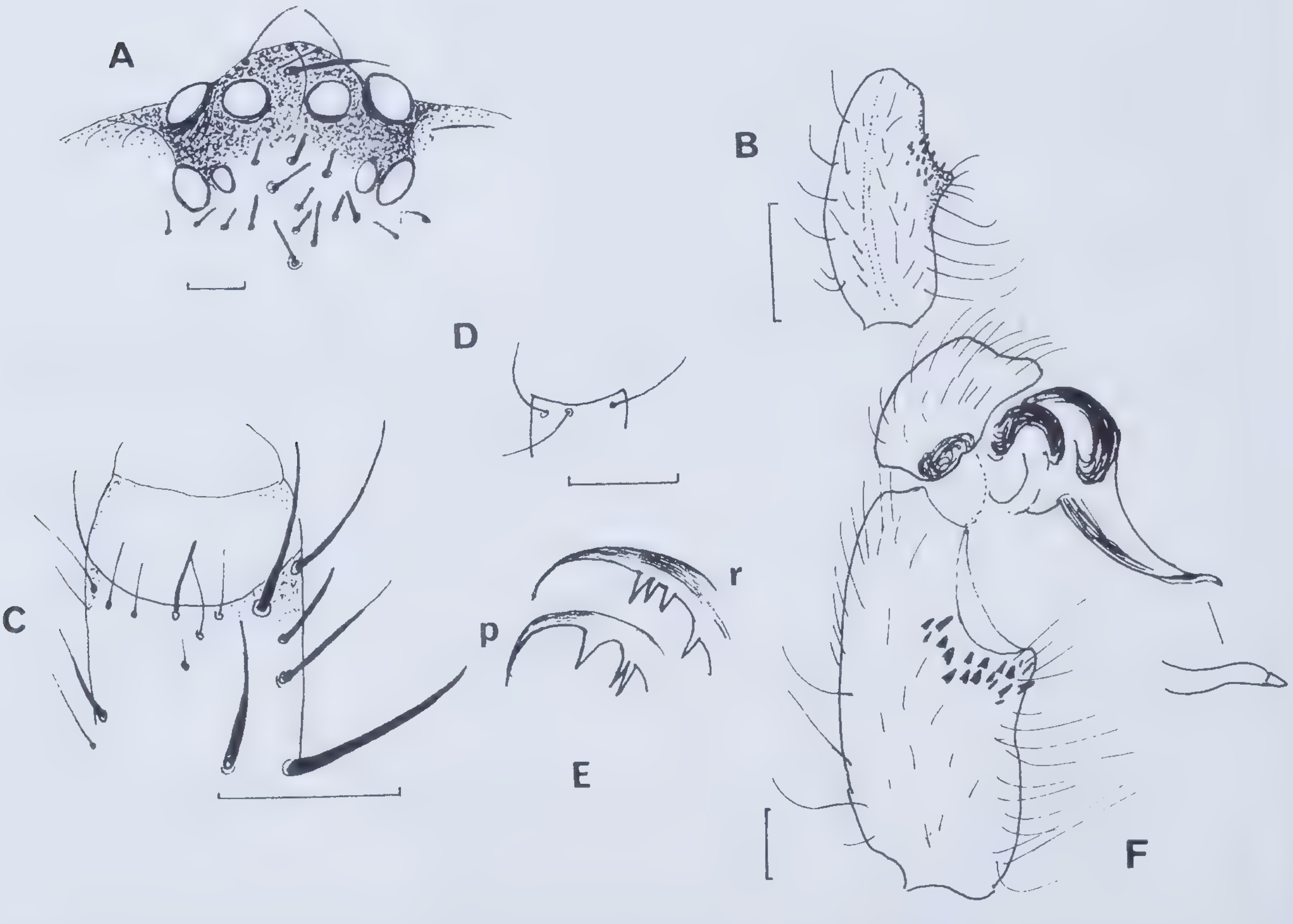

Figure 3. *Arbanitis ballidu* sp nov, male (holotype). **A**, Eyes. **B**, Right palp tibia, retrolateral. **C**, Tibia I, right leg, ventral view. **D**, Metatarsus I, right ventral, apical bristles. **E**, Paired tarsal claws, right leg I, prolateral aspect (p, prolateral; r, retrolateral). **F**, Right palp, tarsus and bulb/embolus and tibia retroventral aspect. Scale bars: A = 2.0 mm; B, F = 1.0 mm; C, D = 0.5 mm; E, not to scale.

Table 2

Leg dimensions of holotype male of *Arbanitis ballidu* sp nov. Leg formula and tibial index (see Petrunkevitch 1942).

Leg formula: 4 / 4.61 1 / 3.22 2 / 3.39 3 / 3.11

Legs	**Fem**	**Pat**	**Ti**	**Mt**	**Ta**	**Total**
I	4.7	2.1	3.3	3.3	1.8	15.2
II	4.4	2.1	3.1	3.3	2.0	14.9
III	3.5	1.9	2.8	3.4	2.0	13.7
IV	5.0	2.3	4.5	5.8	2.7	20.3
Palp	2.2	1.3	2.1	_	0.9	6.5

Width patella I at knee = 0.6. **Tibial index** = 11.1
Width patella IV at knee = 0.7. **Tibial index** = 10.2.

Tarsal claws few teeth; leg I retro claw with one large proximal and 3 even sized teeth, prolateral claw with 2 small proximal and one large distal tooth. *Spines* Some large tapering spines but most spines and bristles are adpressed, rod-like and terminally truncate; tarsi I - III without spines, tarsi IV with 2 (left) and 3 (right) ventral spines.

Leg I lacks apophysis, comb or heavy apical spines; a single, long, tapering pro-ventral spine and one adjacent ventral, slightly smaller, bristle-like spine. Tarsi without spines. *Palp* tibia with slight median swelling but not a pronounced process, with about 20 short spines; embolus tip not distinctively tubular, small terminal "prong".

Habitat

Mixed open, wodjil/heath on yellow sand.

Discussion

The peculiar shiny, waxy-looking, white colour of the carapace of the spiders described is possibly due to deposition of guanine in the basal tissue of the integument. This area is surrounded by a narrow, hyaline or transparent margin, as is typical of the carapace of many species of *Arbanitis* in which the carapace is otherwise dark coloured.

Several other male *Arbanitis* specimens with pale (but yellowish rather than white carapaces) have recently been collected from a site with yellow sand near Buntine (Registration numbers WAM 1996/934,935). Although some morphological features of these specimens are similar to the Ballidu species (for example the undeveloped tibial protuberance with fewer spines on the palp, bristle-like apical spines on tibia I and few teeth on the tarsal claws), they appear to represent another species. Additionally, and since this paper was prepared, a further male specimen of *Arbanitis* with a white carapace, has been found amongst some specimens collected by the late Graeme Smith and simply labelled "Kalbarri, 1982". This specimen has a very distinctive pro-ventral, apical comb of spines on tibia I and clearly represents a fourth species exhibiting the interesting colour pattern. Whether the four species are closely related or have independently developed the colour patten cannot as yet be stated. These specimens, all lodged in the WAM, will be described later along with descriptions of other new Western Australian species of *Arbanitis*.

The remarkable contrasting pattern of glazed white carapace and dark abdomen and appendages of the above spiders may be visually disruptive and hence render the spiders cryptic against a background of white or yellow sand that is partially covered by litter. Assuming that the males wander at night like most idiopid species, the postulated camouflage may be a defence against predation by nocturnal birds, particularly ambulatory ground feeding birds such as curlews and also owls; the disruptive pattern would be equally effective during daylight.

Acknowledgements: I thank M Harvey of the Western Australian Museum for making the specimens available for me to examine and describe and J Waldock and M Harvey for companionship in the field. Most particularly R P McMillan is acknowledged for collecting the first semi-albino.

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Obituary: Joseph Gentilli

(13th March 1912 to 1st August 2000)

Joseph Gentilli has spent the last 60 years in a love affair with research and academic life at The University of Western Australia. This has been a fruitful liaison for both sides. He was one of the founding fathers of the Department of Geography and all there owe a lot to his sustained contribution over the many decades.

Within and outside the University of Western Australia, Joe's work is known far and wide for its original and far-sighted contributions across the discipline of geography, and most particularly in climatology. Indeed his contribution to climatology is formidable. He was responsible for preparing the first accurate climate and rainfall maps for Australia, Western Australia and Tasmania. He was the first to recognize that a regional 'pseudo' or monsoon-like system operated over NW Australia and there were Summer 'Heat Lows' with mean positions located over the Pilbarra in Western Australia and Cloncurry in Queensland. These features are now routinely recognized as being important for understanding climate patterns across northern and central Australia, and whenever you experience humid weather in Summer in Perth, remember Joe, for you are witnessing that these systems have teleconnections to climate systems more widely.

Joe was the first to describe the nature of the Leeuwin Current, a prominent ocean current that brings warm water in Winter along Australia's western coast. This system is of enormous significance for marine life and fisheries in Western Australia.

In 1972 he wrote about the importance of factors in the Indian Ocean leading to the onset of weather patterns in other parts of the World. He was no doubt amused two years ago to see a major conference convened in Perth where this was being 'discovered' and reported.

His synthesis work on climate is particularly well known. His *'Climates of Australia and New Zealand'*, published in 1972, remains a major work in the field. He was the first to do comparative work on climate systems of the southern continents, and from this he was able to show that the Southern Hemisphere was not a simple analogue of the Northern Hemisphere. Typically, he took this a lot further. He looked at the differences across the southern continents and began to ask what were the climate connections between them? This kind of comparative research is a major part of climatological investigation today. It is an essential part of modern forecasting.

He was one of the first to begin looking for evidence of the 'Enhanced Greenhouse Effect' in climate records of Australia, a business that keeps minds active today.

Satellite image of Leeuwin Current (28 March 1989) from The Leeuwin Current, Journal of the Royal Society of Western Australia 74(1991).

Any one of these contributions might be regarded as major advance in its own right. But in parallel with these fundamental discoveries, Joe also investigated the impact of climate variability on many other kinds of systems such as flowering patterns in the native flora, on human health, on wheat yields in WA, and on other phenomena.

Joe also made contributions to other areas of physical geography: in geomorphology and biogeography. He also visited the other 'half' of geography, human geography. In his bibliography there are papers on:

- Economic development in arid lands;
- Regional planning;
- Regions and their characteristics;
- Italian, Swiss and Chinese immigration into Western Australia;
- Refugees in Australia;
- Population changes in Wheatbelt districts of Western Australia;

and in the last few years he became interested in the distribution of privilege, social factors and school performance in metropolitan Perth's secondary schools. Some of these topics reflect his own history, and all reflect his natural curiosity about the world.

The breadth and spread of his scholarship appears in over a 150 papers, books and articles, and these have been written in English, Italian, French and German. He also had a rough reading knowledge of Russian, but surprisingly wasn't game to publish in that language.

Joe once wrote 'I have never decided beforehand what research I shall do – research has always found me, but I gladly say that I never let opportunities slip by'. Indeed he didn't. His academic life was marked by an intense interest in learning through observation, research, checking and analyzing. The success of this approach can be seen in the myriad of national and international awards Joe has received in recognition of his outstanding work and contributions to learned societies.

The other side of Joe's academic life was as a teacher. He believed students to be treasure chests of beautiful things if they are allowed to develop. He saw that the trick for the teacher was to bring out the best without imposing anything. Thousands of students have passed through UWA and many remember him with affection. He stimulated them to learn and develop self-belief. He was an inspiring man.

In 1998, The Royal Society of Western Australia made Joe Gentilli an Honorary Life member, in recognition of his long and distinguished contributions to science in Western Australia.

Professor John Dodson
Department of Geography
University of Western Australia

Journal of the Royal Society of Western Australia

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Management of Granite Outcrops Symposium
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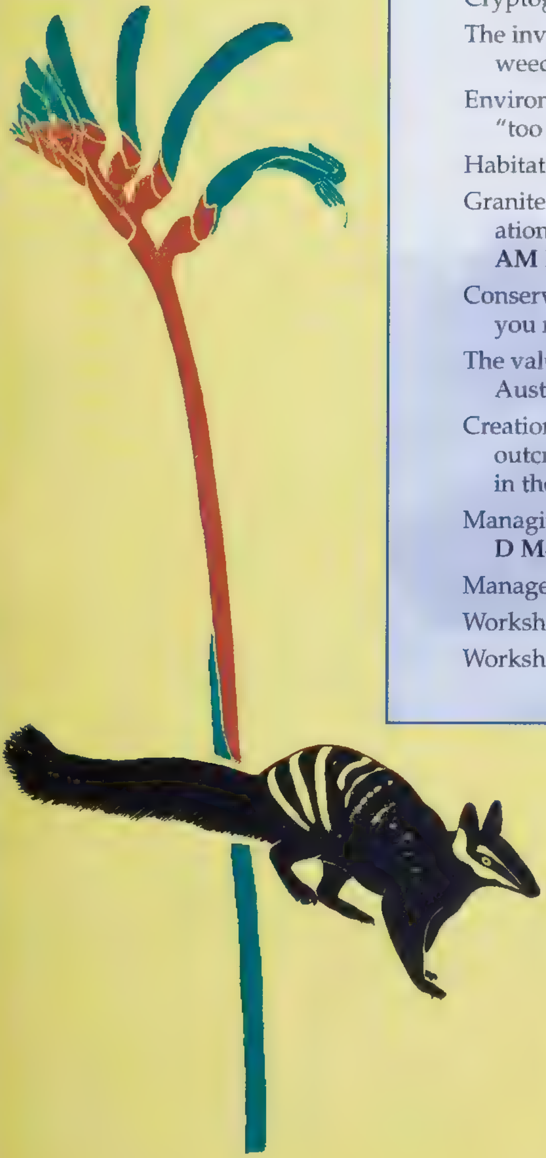

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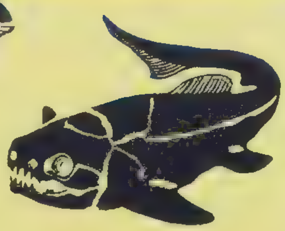

The Royal Society of Western Australia

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The Royal Society of Western Australia was founded in 1914. The Society promotes exchange among scientists from all fields in Western Australia through the publication of a journal, monthly meetings where interesting talks are presented by local or visiting scientists, and occassional symposia or excursions on topics of current importance. Members and guests are encouraged to attend meetings on the third Monday of every month (March - December) at 8 pm, Kings Park Board offices, Kings Park, West Perth, WA 6005.

Individual membership subscriptions for the 1999/2000 financial year are $40 for ordinary Members and $20 for Student and Associate Members. Library, company and institution subscriptions are $60 for the 1999 calendar year. For membership forms, contact the Membership Secretary, c/o W A Museum, Francis Street, Perth, WA 6000.

The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor) and the Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

ISLANDS IN THE BUSH:
Management of Granite Outcrops

Preface

P C Withers[1] & S D Hopper[2]

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A **Granite Outcrops Symposium*** was held at the University of Western Australia on September 14 and 15, 1996, to promote a cross-disciplinary synthesis of current knowledge of granite outcrops and to derive effective guidelines for conservation managers. Following this successful Symposium, a public workshop **Islands in the Bush: Management of Granite Outcrops*** was held from April 16-18, 1999 at Hyden, to provide an overview of management of granite outcrops at a more practical level than the symposium.

The content of the workshop covered diverse management topics relevant to nature conservation, geology and landforms, flora and fauna, aboriginal significance, tourism, heritage, water supply and recreational enjoyment. It also provided a practical opportunity for scientists and the general public to tour granite outcrops, including Wave Rock and the Humps, for first-hand description of aspects of conservation and management of granite outcrops. Presenters ranged from land managers with direct experience in caring for granite outcrops, to nature conservationists and scientists interested in the practical application of their work.

Granite outcrops commonly appear on the landscape as dome-shaped hills with bare rock exposed over much of their aspect. The water catchment so formed by expanses of granite rock, and the associated diversity of microhabitats, make granite outcrops a haven for both plants and animals. World-wide, about 15% of the earth's continents consists of exposed granite, much of which outcrops in the form of inselbergs — ranges, ridges and isolated hills — that stand abruptly from the surrounding terrain like islands in a sea. In Western Australia, granite outcrops form characteristic landforms across much of the gently undulating terrain of the State, and these granite outcrops are of special interest

- geologically, being among the world's oldest rocks,
- hydrologically, providing a source of water in an often dry landscape,
- biologically, as refuges rich in endemic plants and animals, and
- culturally, being vital for aboriginal, colonial and contemporary peoples alike.

Despite these various values of granite outcrops, their conservation is by no means secure. Partly because of the diverse values that are given to granite outcrops, ranging from economic exploitation for rock, to tourism, to nature conservation, the problems with managing granite outcrops are diverse and the task of conserving them for future generations is difficult. Adequate management ultimately depends as much on public participation as government intervention, and the objective of this workshop was to bring scientists, conservationists and the general public together for a broad discussion of conservation issues pertaining to granite outcrops.

As editors, we thank the Royal Society of Western Australia for hosting the workshop, and the Gordon Reid Foundation for Conservation for financial sponsorship, including subsidy of the attendance fees for the general public and assistance with publication of this special issue of the

Journal of the Royal Society of Western Australia.

From top: Mt Arid, WA, A George; Spear Hill, WA, S D Hopper, Kings Park & Botanic Garden; granites, D Blumer; lizard trap on granite outcrop near Woolbale Hills, WA, T Middleton; gnamma on Pildappa Rock, WA, I A E Bayly; *Boryia* on Sullivan Rock, WA, S D Hopper, KPBG; *Otelia* at Twine Reserve, WA, S D Hopper, KPBG; clam shrimp (conchostracan crustacean) *Limnadia*, J McRae, CALM; mygalomorph spider *Teyl luculentus*, B York Main, UWA; water boatman (bug, Hemiptera) *Sigara mullaka*, J McRae, CALM; western toadlet *Pseudophryne occidentalis*, R Johnstone, Western Australian Museum; dragon lizard *Ctenophorus ornatus*, R Johnstone, WAM; mallee *Eucalyptus caesia* and New Holland honeyeater *Phylidonyris novaehollandiae*, S D Hopper, KPBG; black-footed rock wallaby *Petrogale lateralis*, CALM.

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* Both the **Granite Outcrops Symposium** and the **Islands in the Bush: Management of Granite Outcrops Workshop** were jointly sponsored by the Royal Society of Western Australia and the Gordon Reid Foundation for Conservation, WA Lotteries Commission.

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Overview of granite outcrops in Western Australia

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Keywords: inselberg, granites, geology, distribution, Western Australia, plants, animals, conservation

Introduction

One of the objectives of this workshop, and this issue of The Journal of The Royal Society of Western Australia, was to examine the management of granite outcrops from a more applied than academic viewpoint (see Granite Outcrops Symposium, *Journal of the Royal Society of Western Australia*, Volume 80[Part 3], 1997). This paper presents a broad overview of granite outcrops in Western Australia based on the Granite Outcrops Symposium, from a geological, geomorphological and biotic point of view, to provide a foundation for the following papers in this issue on more detailed and specific aspects of management of granite outcrops. Since the Granite Outcrops Symposium, three books pertaining to granites have been published by participants from that symposium, *Rock of Ages* (Bayly 1999a), *Life on the Rocks* (Nikulinsky & Hopper 1999) and *Inselbergs* (Porembski & Barthlott 2000). In addition, Agriculture Western Australia has produced a *Revegetation on Farms Information Kit*, and the Department of Conservation and Land Management has produced two booklets *How to Manage Your Granite Outcrop* (Hussey 1998) and *Exploring Granite Outcrops* (McMillan & Pieroni no date).

Granite outcrops form a complex part of the varied ecosystems in Western Australia, although they are often perceived as isolated rock forms jutting out of the surrounding landscape. They have been formed at varying geologic times, by various processes. They have subsequently weathered into differing major landforms (inselbergs, nubbins, koppies, *etc*), and a wide variety of minor structural forms (pits, basins, *etc*). Not only do granite outcrops form a specialised suite of habitats for animals and plants in their own right (*e.g.* rock pools, meadows, exfoliating rock sheets, rock crevices) but they also merge with the surrounding habitats and form specialised edge habitats, the fringing apron. Thus, the flora and fauna associated with granite outcrops are not only those species adapted to survive and persist on the granite rock habitats, but include many species from the surrounding habitats that seek temporary or permanent refuge amongst the granite rocks, or on the fringing apron.

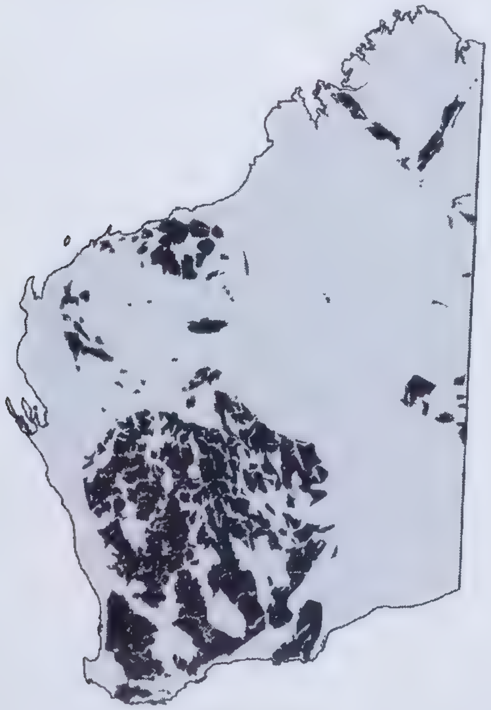

Figure 1. Distribution of granitoid landforms in Western Australia. Redrawn from the hydrogeological Map of Western Australia, Geological Survey of Western Australia (1989).

Distribution of granites

Granite rocks are one of the most wide-spread and abundant types of rock on Earth. Granite forms the bulk of the continental crusts as well as uplifted mountain ranges, whereas the oceanic crust is mainly basalt.

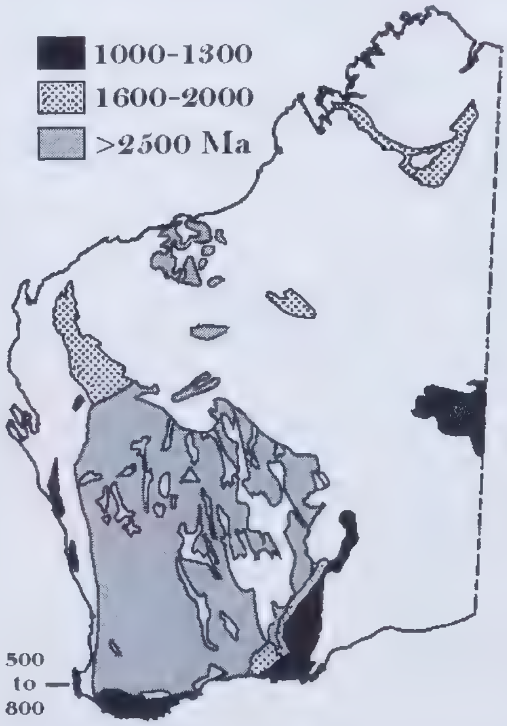

Figure 2. Approximate ages of formation of the main granite outcrops in Western Australia (modified from Myers 1997).

Granite outcrops are distributed widely throughout Western Australia. Although there does not appear to be a specific map of granite outcrops in Western Australia, the distribution of granite landforms clearly indicates a widespread potential distribution of granite outcrop habitats over much of the south-western portion of Western Australia, and to a much lesser extent north-eastern, east-central and northern Western Australia (Fig 1; see also Withers 1997). Much of the western part, particularly the Yilgarn cratonic block (see below), is covered by granite, and there are scattered patches of granite in the East and West Pilbara. There is a pronounced "V"-shaped patch of granite in the Kimberley, and scattered patches of granite along the eastern border of Western Australia, particularly around the Musgrave Ranges.

Origins of granites

The extensive granite outcrops of Western Australia are not of uniform age, but vary widely from over 2500 million years old to less than 1000 million years old (Fig 2; Myers 1997). These varying ages reflect differences in formation of the granite rocks.

The extensive south-western granites are part of the Yilgarn Craton, and were formed 2600 to 2700 million years ago when this craton was generated by assembly of numerous smaller continental crust rafts. The granites of the Pilbara craton are mostly buried by volcanic rocks and the Hammersley banded iron formations.

Other granite outcrops of Western Australia were formed in three major, distinct orogens, representing separate episodes of continental collision of cratons (Fig 3; see Myers 1997). The younger granite outcrops of the Kimberley and Gascoyne regions result from the colliding, about 1600-2000 million years ago, of the Pilbara, Yilgarn and other continents. Two more recent episodes of continental crust collision formed granite in the south of Western Australia. The older of these, the Recherche granite, was intruded about 1300 million years ago by deformation of the Mawson Craton and the West Australian Craton. Even younger Esperance granite, formed about 1180 million years ago, may be largely derived from another episode of compression between the Mawson and West Australian Cratons. The Musgrave granites formed at about the same time through deformation between the Mawson Craton and the North Australian Craton. The granites in the vicinity of Cape Leeuwin are even younger, having formed about 500-800 million years ago.

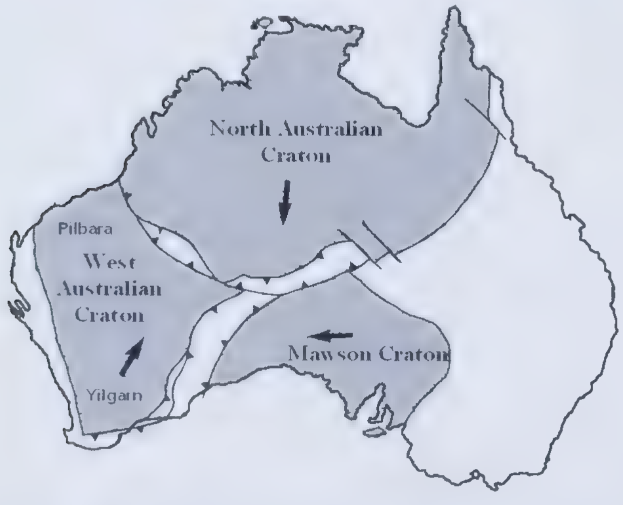

Figure 3. Schematic of the three independent cratons of continental crust with their main directions of movement (modified from Myers 1997).

Granite landforms

The particular landforms typical of granites are not peculiar to granite rock, but are sufficiently characteristic that the underlying nature of the granite rock can often be discerned from afar (Campbell & Twidale 1995). The development of granite landforms is largely due to patterns of weathering, as well as tectonism (Campbell 1997). Weathering by air and water through physical and chemical effects, as well as biological effects, shape granite landforms.

The major landforms of granites include relatively smooth plains as well as the more obvious positive relief features such as inselbergs (Fig 4; Twidale 1982; Campbell 1997). Bornhardts are the basic form of inselbergs, being rounded dome forms of massive bedrock. Nubbins and castle koppies are derived from bornhardts by partial breakdown below the surface of granite sheets to form blocks and boulders (nubbins) or pronounced weathering of vertical fractures (castle koppies). Granite pillars are blocks or towers from which the surrounding regolith has been removed.

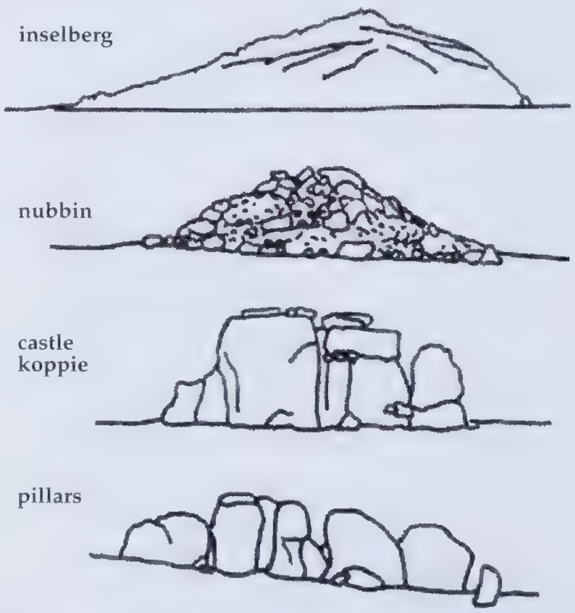

Figure 4. Schematic of major granite landforms (drawn from photographs in Campbell 1997).

The finer details, or minor forms, of granite rocks are mainly formed by weathering, although tectonism creates some features such as A-tents and deposition of weathered materials forms features such as speleotherms (Campbell 1997; Table 1). Rock basins (gnammas) are irregular to circular depressions in solid granite rock (Fig 5). They are often initiated at a shallow weathered depression or on fractures or fracture intersections. Hemispherical pits often form in more homogeneous

Table 1.

Summary of modes of formation for minor granite landforms by weathering, tectonism and construction (modified from Campbell 1997). Note that a number of minor forms are probably convergent, being formed in more than one way.

Weathering	**Initiated at weathering front**	pits	flared slopes
		gnammas	caves
		gutters and grooves	clefts
		flakes and spalls	blocks
		polygonal cracks	boulders
	By partial exposure	rock levees	pedestal rocks
		rock doughnuts	plinths
		fonts	
	Initiated at surface	gnammas	flakes and spalls
		gutters and grooves	blocks
		tafoni	boulders
	By crystal strain	Clefts	gutters and grooves
	By gravitational pressure	gnammas	tafoni
	By intrusive veins	clefts	walls
Tectonic		A-tents	fault scarps
		Blisters	orthogonal cracks
		triangular wedges	
Constructional		speleotherms	boxwork ridges

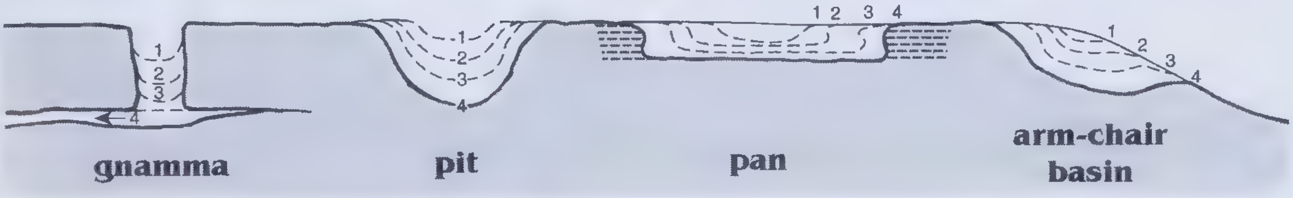

Figure 5. Schematic showing the development of gnammas, pits, pans and arm-chair basins by progressive weathering, indicated by numbers (drawn from Campbell 1997).

granite, and flat pans often form in laminated granite. Arm-chair basins are modified pans or pits, but on steeper slopes. Gutters and grooves develop on recently exposed granite, like gnammas. Flared slopes are often found around the base of hills, and are formed by subsurface weathering followed by removal of the regolith to expose the smooth sloping weathered front. Tafoni are hollows at the base of boulders, formed at the weathering front or by gravitational force of a large boulder sitting on a granite outcrop. In contrast, A-tents (pop-ups) are arched slabs of granite, caused by permanent expansion of a sheet of granite due to release of compressive load. Finally, construction of granite features from weathered sediment is relatively rare, but precipitation of sediments can form silica flowstone, stalagmites or stalactites, and precipitation in fractures then weathering of the softer granite can form a boxwork pattern of small silica ridges.

Granite outcrop biota

It is clear that the times of formation of the different groups of granite outcrops in Western Australia considerably pre-date the presence of existing species of terrestrial vertebrates and invertebrates. Nevertheless, the current distribution of plants and animals on granite outcrops can reflect relictual isolation of ancient species by continental drift (*e.g.* the breakup of Gondwana) as well as more recent (in geological time) evolutionary and dispersal patterns. Some granite outcrop biota are clearly ancient relictual populations. For example the chironomid insect *Archaeochlus*, which is restricted to the granite outcrops in south-western Australia, has congeners found in the Drakensberg escarpment of southern Africa; these ancient Gondwanan remnant populations have been separated for a minimum of 120 million years (Cranston *et al.* 1987; Withers & Edward, 1997). In contrast, the granite-specialist dragon lizards (*Ctenophorus* sp) are much more recently evolved species, from perhaps a Tertiary radiation of amphiboluroid lizards (Hutchison & Donnelan 1993).

Granite outcrops often appear physically to be "islands" in the surrounding landscape, and they have a profound influence on the local plants and animals (Mares 1997). Important aspects of the physical environment provided by granite outcrops for plants and animals include the nature of the substrate, the shelter provided by rocks, and the sources of water that can accumulate on rocky substrates (Fig 6). Plants and animals which are permanent residents of granite outcrops often have adaptations for adhering, or moving over, the bare surface of granites. Weathering of granite produces many special habitats for plants and animals, including exfoliating sheets of granite, water-retaining depressions, and the talus around the base of weathering rocks (Wyatt 1997). Permanent and partial residents of granite outcrops exploit these habitats. The environmental conditions are often harsher on rock outcrops than in the surrounding habitats, with higher

	RESIDENCY		
	Permanent	**Partial**	**Transitory**
SUBSTRATE	➤ lichens ➤ plants ➤ *Teyl* ➤ rock wallabies		
SHELTER	➤ pseudoscorpions ➤ spiders ➤ dragon lizards ➤ rock wallabies	➤ web spinners ➤ mud wasps ➤ frogs ➤ thick-tailed gecko	
WATER	➤ aquatic invertebrates ➤ desiccation-tolerant invertebrates ➤ fishes	➤ tadpoles ➤ insect larvae ➤ water beetles	➤ chironomid midges ➤ birds ➤ bats ➤ kangaroos

Figure 6. Roles of granite outcrops with respect to substrate, shelter, and water, for permanent, partially permanent, and transitory examples (modified from York Main 1977).

temperatures and lower moisture because of the high runoff of water from rocks; the exposed rock outcrop habitats are essentially desert environments scattered among the more mesic surrounds. However, protected, shaded microhabitats that collect rainwater are much more mesic than the exposed granite surfaces, and often the surrounds, and provide temporary or permanent sources of water for permanent, partial or transitory inhabitants.

Granite outcrops generally have a regional influence on plants and animals, increasing the local species diversity (Mares 1997). The biota of granite outcrops includes species that are permanently resident amongst the rocks, as well as species that are permanent or transitory residents. The common appearance of granite outcrops as "islands" in the surrounding landscape, and their distinctive biota, has led many botanical and zoological studies to examined the plants and animals of granite outcrops from an island biogeography perspective (York Main 1997). Granite outcrops are also commonly refugia for plants and animals that previously were more widespread, or during periods of environmental stress (drought, flooding, *etc*) in the surrounding landscape. So, to a large extent granite outcrops preserve a relictual, contracted and fragmented biota.

For plants, the diverse microhabitats on granite outcrops are refugia for both mesic and xeric plants, during climate change (Hopper *et al.* 1997). However, granite outcrops also act as foci for evolution and speciation of plants and animals specialised for the physical and biotic environment provided by these "islands", and are a potential evolutionary "bottleneck" for small, isolated populations. In Western Australia, the flora of granite outcrops shows biogeographic patterns that mirror the whole flora (Hopper *et al.* 1997). In the south-west and pastoral zone, granite rocks have a higher level of endemism than do rock outcrops of the northern zone. In the south-west, an apparent stochastic dynamism of dispersal and local extinction can result in great variability in the flora (orchids) of adjacent outcrops yet a similar flora of widely-separated outcrops. The species that are endemic to granite outcrops may be relictual with no obvious closely related species and therefore have been isolated on the outcrops for a considerable period, may be sister species derived by speciation from allopatric congeners of surrounding habitats, or may be sister species derived by speciation from allopatric congeners of nearby granite outcrops (Hopper *et al.* 1997). Granite outcrops thus may harbour relict species and preserve a record of evolutionary change; for example, the initial stages of evolution in the genetically complex lineages of *Isotoma petraea* are preserved at Pigeon Rock (Bussell & James 1997).

In contrast to the plants, relatively few animals are restricted to granite outcrops but many species use them as a seasonal resource or for temporary refuge during climatic fluctuations (Withers & Edward 1997). The fauna of temporary aquatic habitats on granite outcrops is poorly documented but there is generally a positive correlation between species diversity and volume of temporary pools (Bayly 1997). Such temporary pond fauna may include permanent residents of pools (with passive and poor dispersal capabilities), animals that actively disperse but are still present during the dry season as dormant life stages, actively disperse but have a discontinuous presence in pools (emigrate before pools dry up), or have an exceptional dispersal capacity and rapidly recolonise temporary waters. Some insects, such as the dipteran *Archaeochlus*, lichen-consuming moth larvae and certain grasshoppers, a pseudoscorpion *Synsphyronus elegans*, and some species of the mygalomorph spider *Teyl*, may be restricted to granite outcrops (York Main 1997; Withers & Edward 1997). No fishes or amphibians are restricted to granite outcrops in Western Australia, although many use them as refugia for shelter during dry periods, or for breeding during wet periods (Withers & Edward 1997). Four reptiles appear to be restricted to granite outcrops, three *Ctenotus* dragon lizards and a gecko *Gehyra montium* (Figure 7). No birds are restricted to granite outcrops, although a number of species frequent them in appropriate seasons (Hopper 1981). No mammals are restricted to granite outcrops, although a number of species that are specialised for rock environments (rock wallabies *Petrogale*, long-tailed dunnart *Sminthopsis longicauda*, rock rats *Zyzomys*, rock ringtail possum *Pseudochirus dahli*) frequent granite outcrops (Withers & Edward 1997).

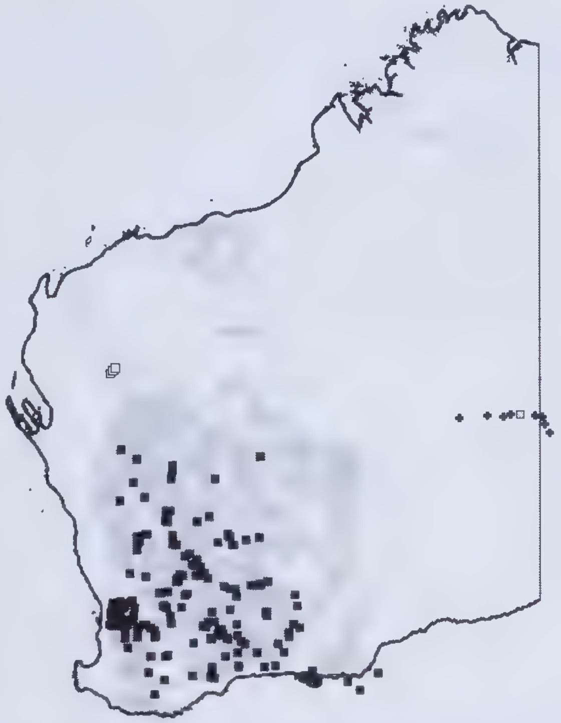

Figure 7. Distribution of three *Ctenophorus* dragon lizards (*C. ornatus* ■; *C. rufescens* ▨; *C. yinnietharra* ☐) and a gecko (*Gehyra montium* ✚) with respect to granite landforms (dark gray shading) in Western Australia (modified from Withers & Edward 1977). Locality data from Western Australian Museum.

Although relatively few animals appear to be restricted to granite outcrops, many other species have been recorded on granite outcrops and it is clear that granite outcrops and their aprons are important as a seasonal resource or temporary refuge during environmental extremes.

Granite outcrops as a human resource

Granite outcrops would undoubtedly have had an important role in the settlement and occupation of Western Australia by Aboriginal inhabitants, as they provide shelter as well as water and food (Bindon 1997; Bayly 1999b). They also are focal points for cultural activities

Early European settlers recognised the value of granite outcrops as a source of water, and since about 1890 approximately 200 locations have been used to collect water runoff (Laing & Hauck 1997). Currently, the Government, the Water Corporation and the farming community continue to use rock catchments as a water source. Some of these may be surplus in areas with piped water, but several rock catchments are connected to the piped water scheme and supplement the total scheme supply.

Conservation

The granite outcrops of Western Australia occupy a very small proportion of the total area of the State, and are rare habitats that are likely to contain rare species of especially plants but also some animals (Hopper *et al.* 1997). Many species also use the fringing apron zone around granite outcrops. Most granite outcrops require management if their local biota is to survive. Physical degradation by rock removal, clearing, invasion by disease, weeds and feral animals, excessive grazing pressure, altered fire regime, and progressive salinisation are but some of the ongoing processes that are likely to affect the long-term survival of granite outcrops and their biota. These diverse problems associated with managing granite outcrops and their apron habitats cannot be reduced to simple recipes (Main 1997). Conflicts between use of granite outcrops by different groups with disparate values for the granites require that adequate management involve both government and public cooperation.

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Mapping granite outcrops in the Western Australian Wheatbelt using Landsat TM data

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Abstract

Granite outcrops are of considerable interest in terms of geomorphology, biodiversity, cultural heritage, recreation and as sources of fresh water in arid landscapes. In the south-west of Western Australia, which is unusually rich in granite outcrops, standard 1:100 000 maps often show granite rocks, as do the vegetation maps published by Beard (1974, 1975a,b, 1976, 1981). While these outcrop locations include many major granite outcrops, no assessment has been made of the completeness of the coverage, and no up-to-date inventory exists.

This paper gives details of an analysis of a sequence of calibrated Landsat TM images for the Kellerberrin scene to identify granite outcrops. The images contain prominent granite outcrops such as Mt Caroline and Mt Stirling. Granite outcrops are mapped by using canonical variate analysis to determine spectral indices (linear combinations of the Landsat TM bands) that best distinguish granite outcrops from other cover types. An interval is then determined for each spectral index that unambiguously identifies granite outcrop. The results are combined to form a 'granite likeness' score for each pixel, and a map of the granite score is produced. Visual agreement with the interpretation based on aerial photos suggests that there is the potential to produce an atlas of Western Australian granite outcrops based on remote sensing imagery.

Keywords: mapping, granite outcrops, Landsat TM, spectral indices

Introduction

Granite outcrops cover 15% of the earth's surface (Twidale 1982). Western Australia is unusually rich in outcrops, which are of considerable interest in terms of geomorphology, biodiversity, cultural heritage, recreation and as sources of fresh water in arid landscapes (Withers & Hopper 1997; Bayly 1999; Nikulinsky & Hopper 1999).

In the south-west of Western Australia, standard 1:100 000 maps often show granite rocks, as do the vegetation maps published by Beard (1974, 1975a,b, 1976, 1981). These outcrop locations, which have been identified visually from aerial photographs, include many major granite outcrops. However, no assessment has been made of the completeness of the coverage, and no up-to-date inventory exists.

The Remote Sensing and Monitoring group in CSIRO Mathematical and Information Sciences (Floreat Park) is using long-term sequences of carefully rectified and calibrated Landsat TM imagery to map and monitor land condition in the WA wheatbelt. Of special interest is the spread of salinity and the status of vegetation (see, for example, Wheaton *et al.* 1992; Wheaton *et al.* 1994; Evans *et al.* 1995).

This paper gives details of an analysis of a sequence of calibrated Landsat TM images for the Kellerberrin scene to identify granite outcrops. We investigated this area because it contains prominent granite outcrops such as Mt Caroline and Mt Stirling, and as a preliminary study to establish the feasibility of producing an atlas of south-western granite outcrops from remote sensing imagery.

We first provide brief details of the Landsat scenes, including image rectification, registration and calibration. Then, granite outcrops are mapped by determining spectral indices (combinations of the Landsat TM bands) which distinguish granite outcrops from other cover types. Finally, the indices are combined to form a 'granite likeness' score for each pixel, and a map of the granite score is produced.

Landsat TM and ground data

The area studied is the Landsat TM scene for Kellerberrin (path 111, row 082) in the WA wheatbelt. The following four scenes are analysed: 2 February 1990; 28 January 1994; 3 February 1996; and 7 January 1998.

The January 1994 scene was first rectified to the WA Main Roads Department Regional Roads database. The rectification approach adopted uses north-south and east-west road segments, and incorporates image overlap with adjacent scenes (see Campbell *et al.* 1999). This approach has produced a sixteen-scene 'mosaic' in which the roads on the Landsat images generally agree to within less than one pixel (<25 m) with the GPS-recorded road position.

The remaining (target) images in the sequence are then registered to the January 1994 (reference) image by selecting a sequence of high-contrast ground control points (GCPs) on the two images, and using cross-correlation matching (Campbell 2000) to find the best sub-pixel match in the target image for each GCP in the reference image. The images are resampled using cubic convolution (see, for example, Schowengerdt 1997, 350).

The third stage in the process is to calibrate the images so that the same condition on the ground has the same recorded value on the rectified satellite image. This is done by selecting pseudo-invariant targets, and using robust regression to relate the values on the target images to those on the reference image (Furby & Campbell 2000).

The Landsat TM satellite records values in 30 m x 30 m pixels over a 185 km x 185 km area in six spectral regions: blue, green, red, near infra-red (IR) and two mid-IR bands (see, for example, Richards 1986, 13). Various three-colour displays can be produced by assigning the spectral bands, or combinations of them, to the three colour guns on the image display (Richards 1986, Section 3.2). After image calibration, it is expected that the granite rocks will not change in 'colour' over time for the various colour displays, whereas surrounding bush and farm areas will.

Identifying granite outcrops

The next stage in the analysis is to determine linear combinations of the Landsat spectral bands (referred to here as spectral indices) which best distinguish bare granite outcrops from other cover types. The approach adopted is canonical variate analysis (see, for example, Richards 1986, Section 10.4.2; Campbell & Wallace 1989).

Briefly, training classes are defined for the various cover classes of interest, and linear combinations of the spectral bands are determined to minimise the between-class variation for the resulting canonical variate scores relative to the within-class variation. Subsequent linear combinations are chosen to be uncorrelated between- and within-classes with previously determined sets of scores. As noted above, the approach requires training classes to be located for granite outcrops and other cover types.

There are several large granite outcrops in the study scene, and these are used to define training classes. The bare granite areas are clearly identifiable in aerial photos taken over the area in October 1994 (see, for example, Fig 1A, which shows an aerial photo for Mt Stirling 6478125N, 558325E). Fig 1B shows a three-colour display of bands 7, 5 and 4 (in red, green, blue respectively) for the January 1998 Landsat TM image. For each of the four scenes, twenty-seven training classes were extracted from regions of bare granite rock, which are identifiable in the three-colour display. Twenty classes were extracted from bush-covered areas of the outcrop, and fifteen classes were identified in adjacent areas (including areas from a chain of salt lakes). Fig 2A shows a plot of the class means for the first two canonical variates for the January 1994 data. A plot of simplified forms of the vectors in Figure 2B gives essentially the same configuration. The first canonical variate separates bare granite outcrop from bush-covered sites, while the second canonical variate separates granite outcrop from salt-lake sites. For these data, there is separation between the granite outcrop sites and the rest, though for other dates there is some confusion between the granite outcrop sites and the bush and salt-lake sites towards the top right of the cluster of granite outcrop sites. Examination of the aerial photos and various enhancements of the TM images suggest that the sites are correctly labelled, and that there is occasionally some spectral confusion between a few granite outcrop sites in the region of overlap.

The contributions that the various bands make to the identification of granite outcrop sites can be assessed by evaluating for all possible subsets the degree of separation between the granite sites and the remaining sites. For these data, bands 4 (near IR) and 6 (mid IR) provide much of the separation.

Calculating a granite index

Examination of the canonical variate (CV) plots in Fig 2 for the January 1994 data and similar plots for the other dates shows that for each date, there is a region in CV space which unambiguously identifies bare granite outcrop. There are also regions that clearly exclude bare granite outcrop. Finally, there are 'transition' zones where the identification is inconclusive.

One approach for identifying regions of bare granite outcrop is to determine an interval for each spectral index which unambiguously identifies granite outcrop; there are two indices for each of the four dates. If the index value falls within the granite interval for that index, then 1 is added to a granite score, and zero otherwise.

For the plot in Figure 2B, the first index is given by –3 x TM2 – TM3 – 9 x TM4 – TM5 + 17 x TM7. If the resulting index is greater than 375, then 1 would be added to the granite score. The second index is given by 5 x TM1 – 14 x TM2 + 14 x TM3 + 20 x TM4 + 2 x TM5 - 8 x TM7. If the resulting index is less than 1830, then 1 would be added to the granite score. The granite score can then be displayed as an image; the higher the score, the greater is the confidence that a pixel is bare granite outcrop. Fig 1C shows an image of the resulting score for the Mt Stirling region.

There are several extensions to the approach which are being considered. The index-based approach can be modified to replace the 1-0 value for each index by a value which varies between 1 and 0. This can be done by adding a transition interval, in which the value changes smoothly from 1 to 0, to give a "probability" of granite. The resulting scores can then be combined using a rule-based system. Campbell & Woodgate (2000) have proposed a similar approach for estimating tree clearing for the Australian Greenhouse Office.

Another aspect that needs to be considered is the spatial pattern of the granite score. If the neighbouring pixels have a high score value (close to eight in our study), this should reinforce the value for the central pixel. If the neighbouring pixels have a low score, and the central pixel has a value, of say, six, then this should weaken the likelihood that the central pixel is granite outcrop. A simple approach would be to calculate a neighbourhood confidence factor, say using the sum of the neighbourhood granite score values divided by the maximum possible sum, and then multiply the granite score for the central pixel by this neighbourhood weighting. This can be done for several iterations to obtain a neighbour–modified granite score. More sophisticated forms of neighbour weighting can be

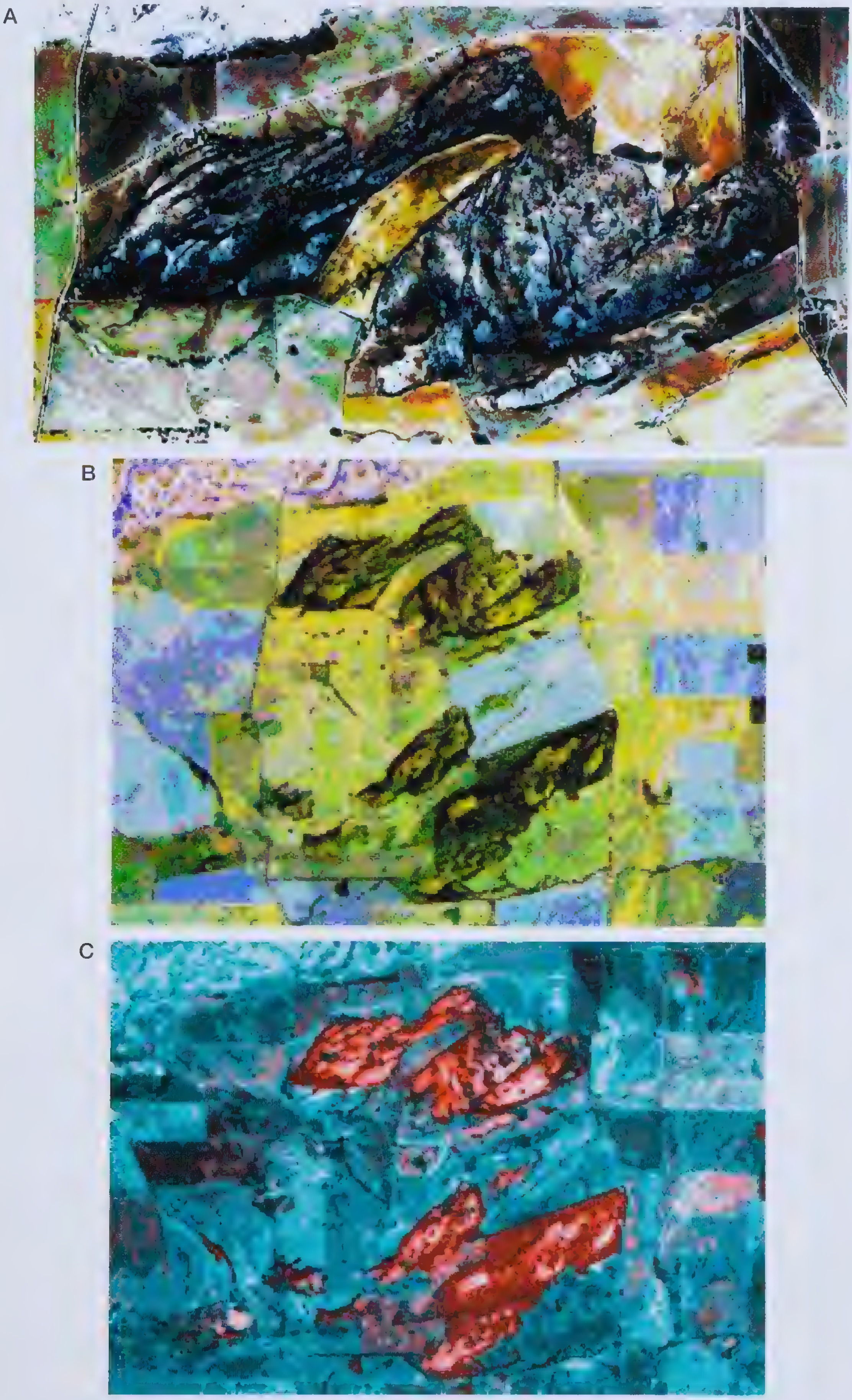

Figure 1. A: 1:25 000 aerial photo for Mt Stirling; 21-10-94. **B:** Three-colour image for Landsat TM data for January 1998 – band 3 assigned to blue gun, band 5 to the green gun and band 7 to the red gun. **C:** Image of granite score for Landsat TM data; brighter areas indicate higher granite score.

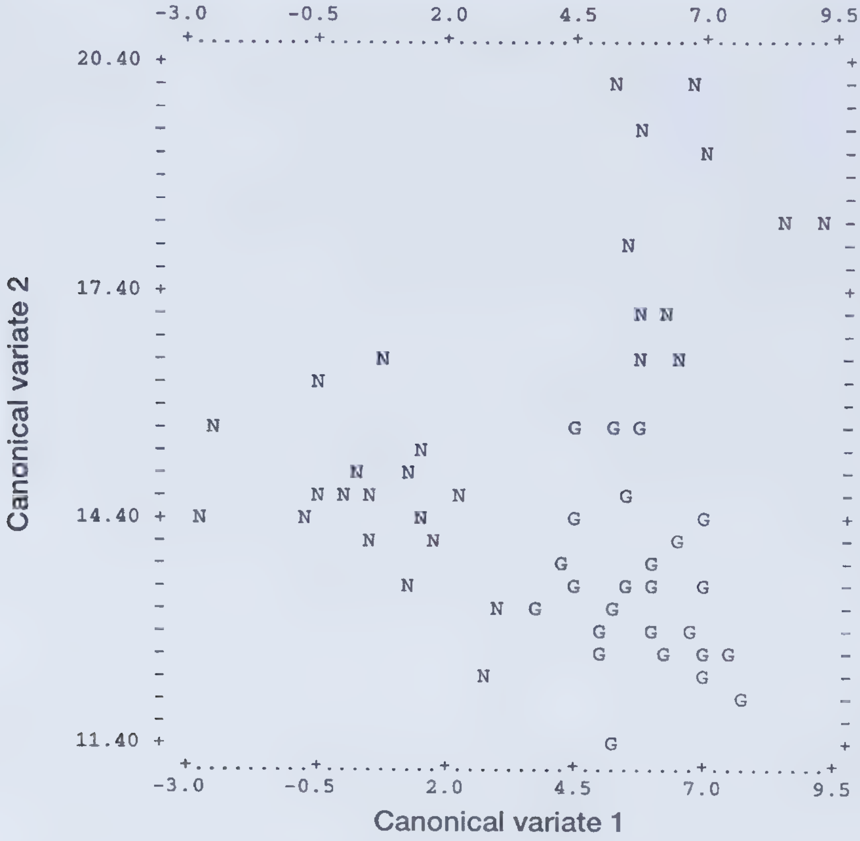

Figure 2. A: Plot of canonical variate class means for January 1994 TM data. G denotes granite outcrop, N denotes non-granite sites. The two canonical vectors are
(0.080 -0.051 0.103 -0.239 -0.027 0.141) and (0.103 -0.215 0.253 0.071 0.016 -0.118)

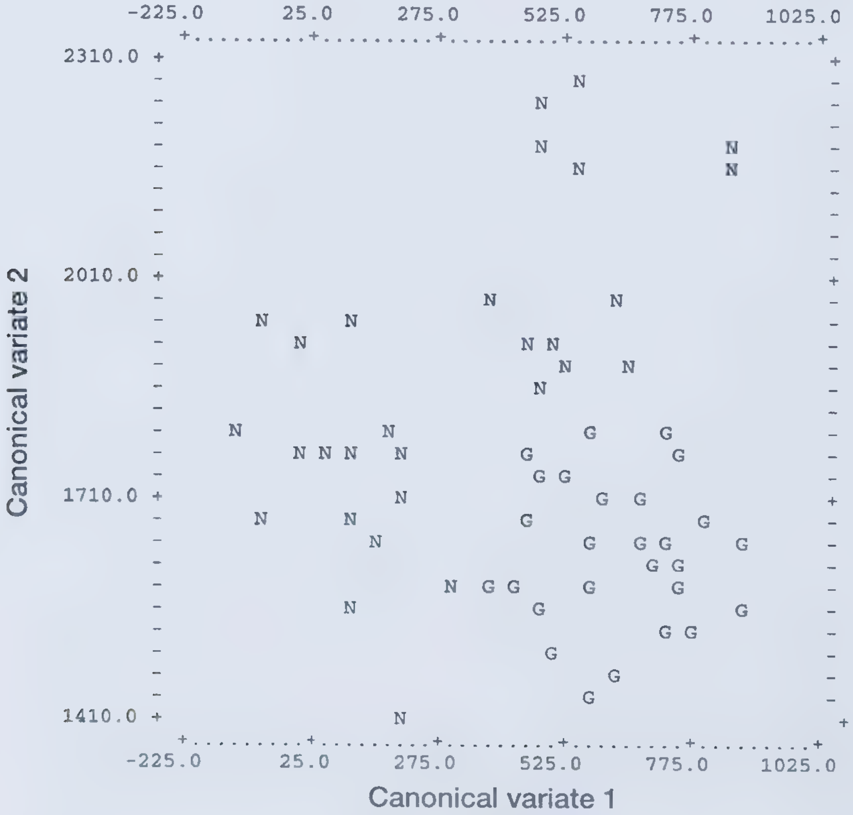

Figure 2. B: Smoothed canonical vectors and plot of canonical variate class means for January 1994 TM data. G denotes granite outcrop, N denotes non-granite sites. The two smoothed canonical vectors are
(0.00 -3.00 -1.00 -9.00 -1.00 17.00) and (5.00 -14.00 14.00 20.00 2.00 -8.00)

formulated, which take into account the actual distribution of the granite score values in the neighbourhood.

The result is again a granite score map. This can be displayed as a threshold map showing only those areas in which the spectral indices unambiguously identify bare granite outcrop. Alternatively, the varying degrees of confidence can be displayed in different colours, perhaps allowing better field validation of the accuracy of the mapping.

We see scope in pursuing these lines of investigation through a combination of ground-truthing and extending the geographical coverage across other landscapes in south-western Australia where granite outcrops are common. The potential to produce an atlas of Western Australian granite outcrops based on remote sensing imagery is encouraging, and merits further analysis.

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Granite outcrops: their utilisation and conservation

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Abstract

Granite, which is exposed over about 15% of the continental areas and is especially prominent in many parts of Western and South Australia, has many attributes which are useful to Humankind. Granite outcrops are useful for quarrying, as catchments in water conservation schemes, as tourist attractions and as recreation areas. Many are of great scientific interest. Granite also has properties which render occurrences hazardous. Granite in contact with water rots easily, slopes tend to be unstable, and blocks of fresh rock are susceptible to displacement by earth tremors. Human interference with slopes introduces and augments problems. Management plans for granite rocks ought to take account of the attributes of particular sites, the merits of competing claims, and possible hazards.

Keywords: granite outcrops, water conservation, quarrying, ecotourism, edutourism, recreation, science

Introduction

Granite is the prime constituent of the continental crust, and though extensively masked by a veneer of volcanic and sedimentary rocks is nevertheless exposed over about 15% of the continental areas. Granite plains and hills are commonplace in the shields and cratons which form the ancient cores or nuclei of the continents. They are also prominent in orogens or fold mountain ranges (*e.g.* Wilhelmy 1958; Godard 1977; Twidale 1982a; Vidal Romani & Twidale 1998; Ikeda 1999; Twidale & Vidal Romani 2001).

In Australia, granite forms extensive outcrops in various of the shields and cratons (*e.g.* the Yilgarn and the Pilbara blocks, in Western Australia, Eyre Peninsula and other parts of the Gawler Craton in South Australia) and is also well represented in mountainous regions such as the Eastern Uplands (Palfreyman 1984). Many well-known uplands and hills like Mt Kosciusko, Mt Buffalo, Wilson's Promontory and Mt Augustus are granitic. Moreover, because it is a hard or resistant rock when dry but is readily altered when in contact with water, fractures in the rock have been weathered by meteoric and ground waters to produce dramatic formations such as some of the Devil's Marbles (Fig 1A). Also, when it is fresh, granite is brittle and cracks easily under stress, again producing spectacular features such as split rocks and A-tents, or pop-ups (Fig 1B). Furthermore, many granite exposures have been intricately sculptured to give cavernous forms such as Remarkable Rocks on Kangaroo Island, and flared slopes such as Wave Rock on Hyden Rock (Fig 1C). Add to these such random erosional forms as the natural coastal arch at Albany, the dramatic wedge and sheet of rock exposed at West Beach, near Esperance, the huge boulder known as The Leviathan, in Victoria, and the sheer simple grandeur of the many granite domes (Fig 1D) that occur in many parts of the country, and it is not surprising that many granite outcrops are tourist and recreational attractions at national and local scales.

Positive attributes

Granite has many other positive attributes and qualities. Though by definition consisting mainly of quartz and feldspar, granites vary in colour and crystal size and many are aesthetically pleasing. When polished, it makes a beautiful stone with hues of rose, pink and mauve, and in some instances, with large crystals (phenocrysts) set in a fine-grained ground mass. Thus many granites have been used for monumental purposes such as the facings of public buildings, paving and headstones. The crushed rock is useful as ballast and gravel. Massive granite is impermeable, so that outcrops make good catchments and storage areas which are especially valued in this, the most arid of the inhabited continents. Moreover, the development of some granite forms, such as flared slopes and stepped bornhardts or inselbergs, has implications for general theories of landscape evolution. Some sites are of scientific interest and importance not only to Earth scientists but also to biologists, for granite hills offer a wide variety of habitats and niches for plants and animals, as well as features attractive to casual visitors.

For these reasons, granite outcrops and landforms are regarded as resources which can be utilised in a variety of ways; they are subject to the competing, and in many instances mutually exclusive, interests of quarrymen, water conservationists, tourist operators (both organised and local), biological conservationists and other scientists, and, justifiably, ordinary folk who cherish local hills as picnic spots and for other recreational purposes.

Potential hazards

On the other hand the specific character of granite weathering and regoliths introduces special and additional risks. Fresh granite is impermeable, but rapidly alters when in contact with water. Thus the mantle of weathered rock (the regolith) characteristically meets the underlying fresh granite in a sharp interface known as the weathering front. The regolith, consisting

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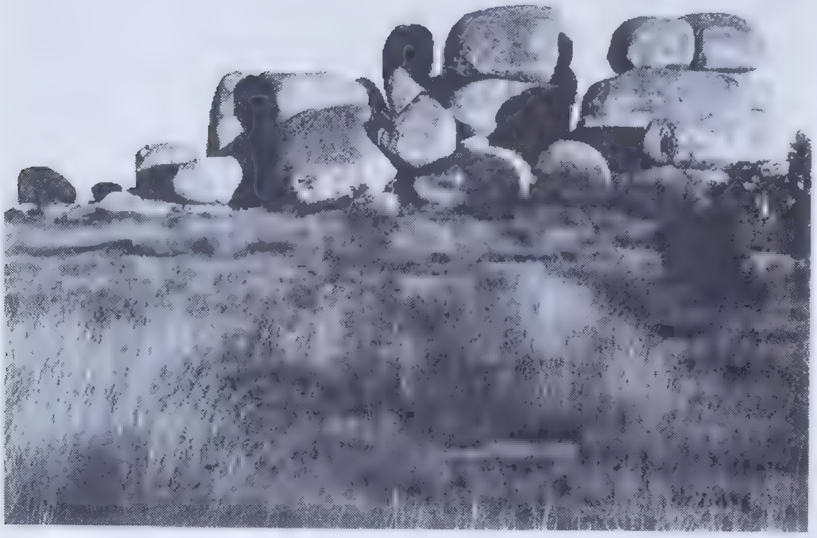

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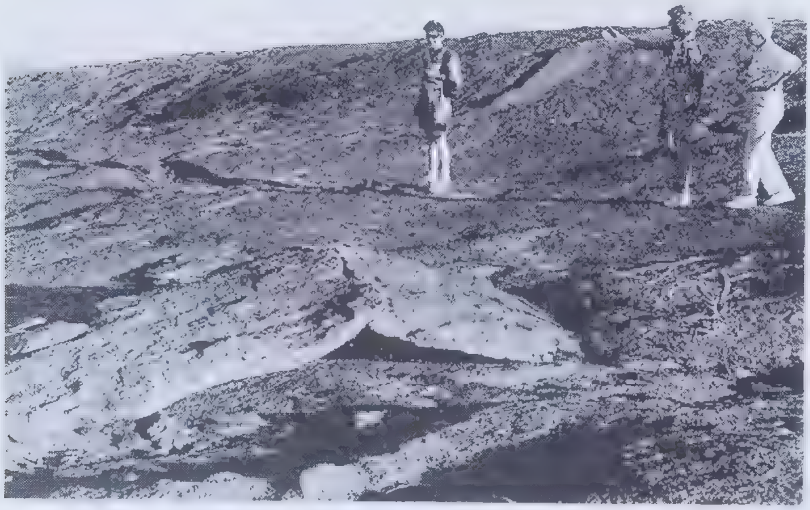

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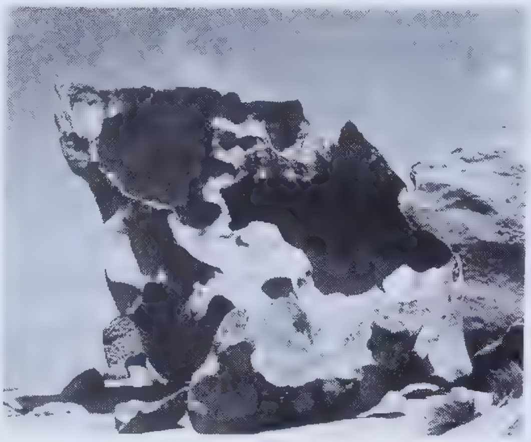

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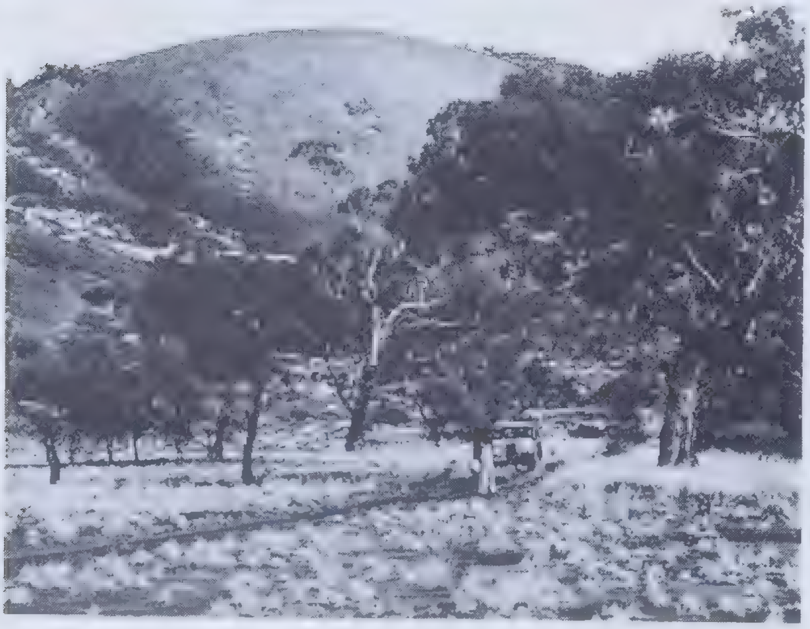

Figure 1. A: Part of the Devils Marbles, Northern Territory. **B:** A-tent, or pop-up, on Bald, or Murray, Rock, east of Hyden, Western Australia, Western Australia. **C:** Alveolar weathering, Remarkable Rocks, Kangaroo Island. **D:** Mt Lindsay, north-west of South Australia (Geological Survey of South Australia).

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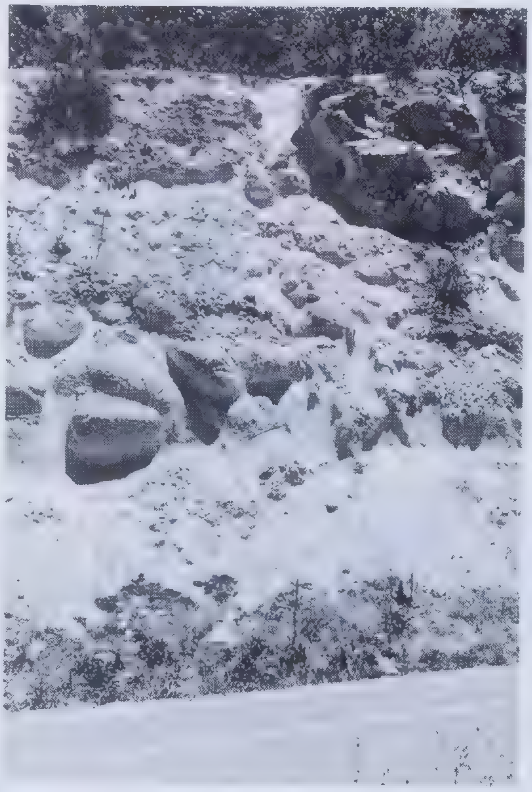

Figure 2. Granite regolith with core-boulders, Snowy Mountains, New South Wales.

of a mix of quartz and clay rests on a surface of fresh rock. Moreover the weathering of granite is frequently incomplete so that the regolith typically consists of boulders (corestones or core-boulders; Scrivenor 1931) and blocks of fresh granite sitting in a matrix of quartz and clay, or just clay (Fig 2). On slopes, and especially steep slopes of course, this is a dangerous situation. Several hazardous situations can be identified.

- First, meteoric waters percolate through the regolith and run along depressions in the impermeable weathering front and form underground streams. Sand and clay fall into the stream from the sides and roofs of such subterranean channels. Eventually the undermined regolith subsides into the channel. The clay-quartz matrix tends to liquify and lose strength. This was the basic cause of the Thredbo (NSW) disaster of July 1997. If there are numerous large blocks and boulders, then the removal of the matrix may cause them to collapse and settle against each other forming irregularly shaped caves, such as have been recorded from Malaysia, Australia, the USA and Guyana; but again there is the potential for inducing settling and surface subsidence. These tendencies are increased if, for any reason such as road construction and drainage works upslope, water is channeled into or on to the regolith.
- Second, following heavy rains or other large accessions of water, or shaking during an earth tremor or earthquake, the entire slope may lose cohesion and fail, carrying downslope large volumes of clay and sand and the contained core-boulders.
- Third, human interference with the regolith such as clearing of trees and/or cutting away the toe of the slope (road construction, land development) causes the regolith to become unsupported or unbuttressed, again leading to failure and the mass movement of debris. Thus, at Paya Terubong on Pulau Penang, West Malaysia, tall apartment blocks (Sun Moon City) were constructed on a granite platform excavated at the base of a high, steep-sided and wooded granite ridge, and a car park was provided by cutting into the base of the slope. On 28 November 1998, a major landslide on the slope above one of the apartment towers carried sand, clay and huge core-boulders (one some 10 m diameter) downslope, burying and crushing a number of parked cars (all fortunately unoccupied) and reaching within about 10 metres of one of the tower blocks. The reason the landslide developed at the time it did (heavy rains, earthquake) is not known, but over the previous two years there were warning signs such as small blocks falling down the slope and the development of what were locally called "waterfalls" (small springs due to water percolating through the regolith, encountering an obstacle such as a core-boulder and emerging under pressure).
- Fourth, the sheet structures typical of many granite outcrops pose further problems, for detached slabs can slip downslope as a result of rains or earth tremors, or where the lower slopes have been undermined or steepened either naturally or by human activities (Fig 3). Thin sheets may buckle either under gravity or as a result of compression associated with earth tremors and 'quakes (Trudinger 1973; Twidale & Sved 1978; Bowling & Woodward 1979; Bourne & Twidale 2000). This can cause dislocation of slopes, with negative implications for quarrying and for dam and pipeline construction. Dipping sets of orthogonal joint systems introduce similar dangers in coastal cliffs, road cuttings, and so on.

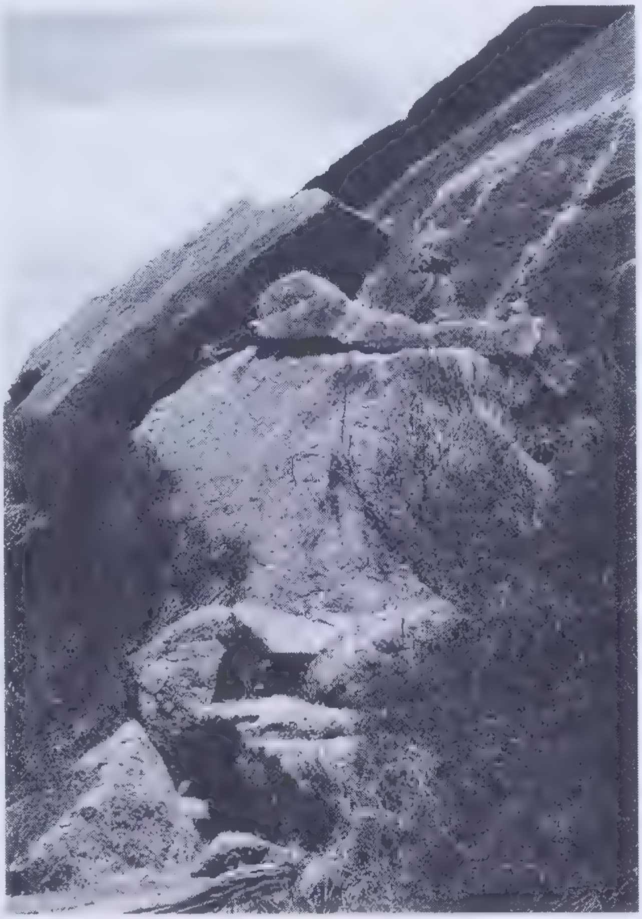

Figure 3. Slipped slab at Kokerbin Hill, Wheatbelt of southwestern Western Australia.

- Fifth, frequently the rock in which granite hills are eroded is in compression, with implications for quarrying and other engineering procedures (Vidal Romani & Twidale 1999; Twidale & Bourne 2000a).

Possible uses of granite outcrops

Quarrying

Quarrying is essential for our lifestyle (gravel for roadbuilding, ballast for railways, building and monumental stone). It generates considerable employment and income. Quarrying is also useful for professional geologists, for it provides clean exposures of rock. Quite understandably in view of the recent and continuing but inevitable rural downturn in employment (inevitable because of various technological advances both general and agricultural) and the stress thus placed on country towns and rural populations, local authorities are, quite properly, examining every new employment possibility; of which quarrying is one.

Unfortunately, quarrying is irreversible. Once gone, the hills quarried cannot be replaced. Moreover, the clean-up record is unimpressive, and more likely than not the natural feature will in time be replaced by a hole, possibly flooded, with a jumble of blocks and with various constructional and industrial debris scattered around.

The quarry industry is not labour-intensive. Modern procedures, involving drilling, blasting, burning and the use of heavy trucks and cranes, are noisy and dirty. They are unhealthy, not only through accidents, but also through such ailments as silicosis and noise-induced deafness (*e.g.* Noor 1988). The incidence of silicosis in quarry workers can be drastically reduced or eliminated by the introduction and implementation of adequate dust extraction, water sprays to settle dust, compulsory use of respirators, monitoring health checks, and education, but it is difficult to ensure implementation. For example in granite quarries in Selangor, West Malaysia, despite government regulations only 14% of workers regularly used the respirators supplied and 47% never used them at all, for they were considered too uncomfortable to wear in the prevailing heat. Consequently some 4% of workers contracted silicosis (Noor 1988); this is not a high proportion, but in our industrial and legal climate it is potentially expensive as well as personally tragic. More telling, in Selangor 79% of quarry workers suffered noise-induced deafness in some degree. Thus, apart from more obvious and immediate hazards in the shape of rock bursts, falling slabs and accidents with explosives, those encouraging quarrying should be aware of long-term health risks and must not dismiss or fail to disclose them.

The benefits and drawbacks of quarrying in the short, medium and long terms need to be weighed against alternative employment possibilities, and if quarrying is a favoured option then great care needs to be taken in selecting the hills that are to be quarried in light of local, regional, national and international needs, possibilities and motives.

It is questionable whether district or shire councils should be actively involved in promoting, much less having a financial interest in, a quarrying venture. They are responsible for the total well-being of a district, yet if they have power to make decisions concerning a venture in which they have a financial stake, then a conflict of interest situation surely arises? For example, if the council or its officers favour a proposal, full disclosure of aims and implications may not be forthcoming, the precise extent and locations of quarrying may not be fully made known, or the nature and extent of possible health problems may remain unmentioned or understated until a formal and legally binding decision has been taken, simply in order to avoid opposition. Any adverse health effects may not become evident for 25 years or so, when the decision-makers may well have moved on, leaving the community to carry any costs arising from the venture; and similarly to bear clean-up costs. But the major consideration with quarrying is that it is irreversible; once done there is no going back, no time for regrets, no possibility of taking advantage of hindsight.

Water conservation

Water conservation has long been practised in arid and semiarid Australia. Aboriginal people, Afghan camelmen and early shepherds took advantage of the gnammas (or rock basins) characteristic of granite outcrops, cleaned them out and in some instances covered them with a rock slab to save life-giving water. They also built low walls to dam shallow valleys, and created storages where none existed before by constructing inverted roofs draining into tanks. Some of the latter are still in use and are, of course, independent of granite hills or any other uplands.

Whereas the early reservoirs were natural, small and received runoff from limited areas, later users constructed reservoirs to utilise very large catchments based on granite hills and platforms, augmented by diverted runoff (see *e.g.* Twidale & Smith 1971; Laing & Hauck 1997; Fig 4A,B). Some, like those at The Humps, near Hyden, in the Wheatbelt of Western Australia, and many of those on northern Eyre Peninsula, were designed and constructed by government agencies. Many were built during the Depression years of the 'twenties and 'thirties and in response to the needs of stock on the newly opened wheat and sheep country of the southern States. Many are minor works of engineering art (Twidale & Smith 1971). Other water conservation works, like the diversion walls constructed high on Hyden Rock, and especially that located immediately above Wave Rock, are not pleasing to the eye; the needs of the time dictated the area of catchment enclosed and outweighed any aesthetic considerations. In passing it may be noted that the Hyden Dam, as well as the diversion walls, are located between or amidst zones of recent tectonic disturbance (Twidale & Bourne 2000b; see also Kiersch 1964).

Other conservation schemes are privately owned and constructed. Some are elaborate like that at Ucontitchie Hill, north-western Eyre Peninsula, whereas others are simple and involve collecting water from only a few square metres of bare rock surface (Fig 4C). Some serve a district, like that at The Humps which supplies Hyden township. By contrast, in the 'thirties and 'forties, water from the Pildappa Rock tank, north of Minnipa, on north-western Eyre Peninsula (Fig 4B) was piped many kilometres to various neighbouring homesteads and troughs, and that at King Rocks, east of Hyden, serves several adjacent farms. By contrast, many others, like that at Dumonte Rock, near Wudinna, partially meets the needs of a single farm.

The elaborate conservation schemes constructed on north-western Eyre Peninsula in the years 1913-1932 were allowed to fall into disrepair from the early 'sixties through the 'eighties with the completion and renovation of the Tod River Pipeline, but with increasing demand for water for stock some are being brought back into service, mostly through private repair and maintenance.

The diversion of runoff into storages reduces the recharge of groundwaters, and in some areas this can be critical. For example, Streaky Bay, the small farming, fishing and tourist centre on the west coast of Eyre Peninsula, derives its water supply partly from home storage tanks into which roof runoff is drained and partly from the adjacent Robinson Basin. Here, a thin layer of freshwater derived from rainfall floats on denser saline waters (see Segnit & Dridan 1938; Shepherd 1985). Any conservation on granite outcrops would disturb an already delicate situation.

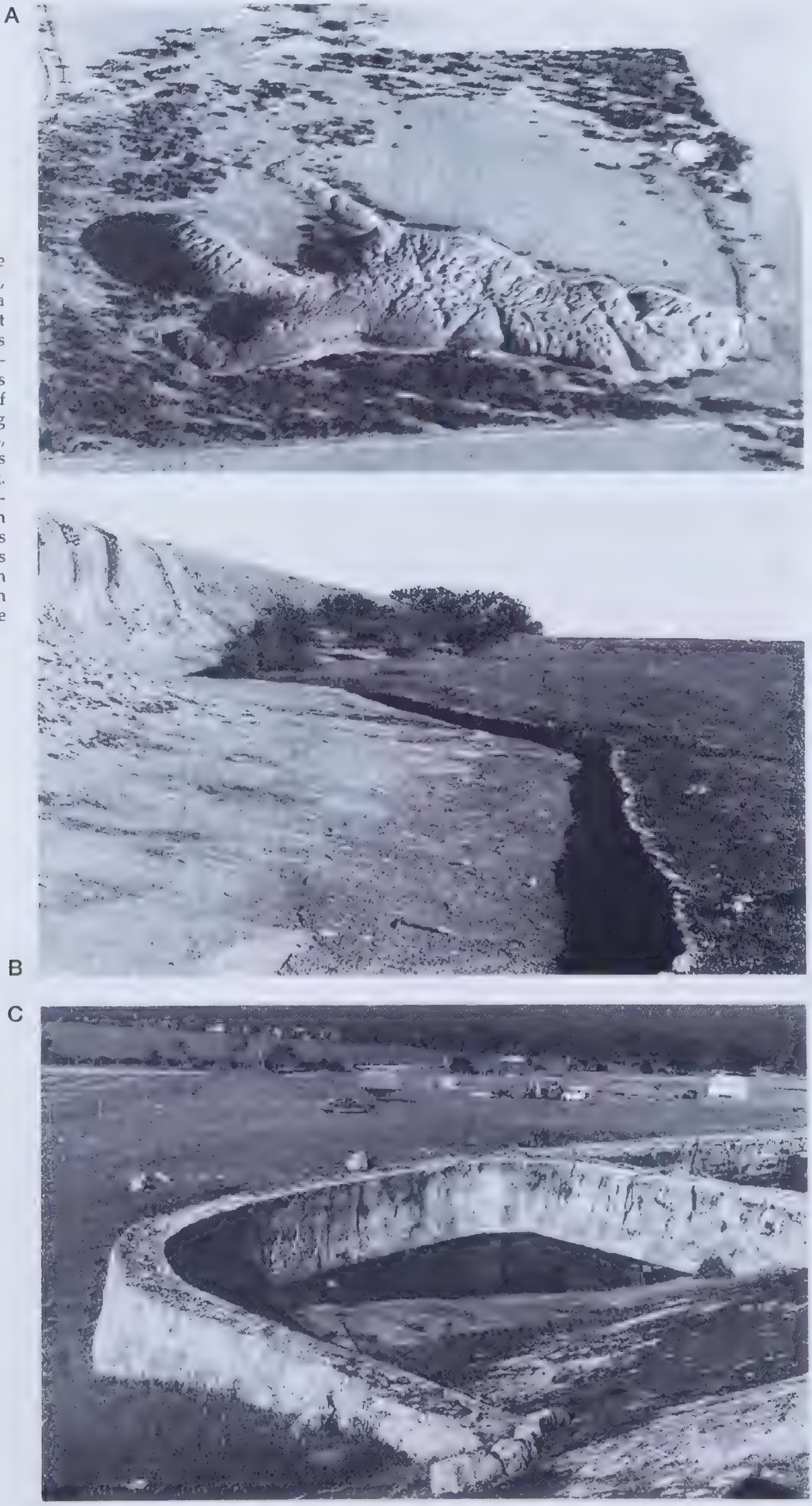

Figure 4. A: The compact surface of Pildappa Rock, near Minnipa, north-western Eyre Peninsula seen here from the south, is about 400 m from west to east and is used as a catchment; a half-million gallon storage tank is seen at top right. **B:** The runoff of Pildappa Rock is diverted along the base of the hill by low walls, which channel water into drains and thence into the storage tank. **C:** Tank at Kolballa Hill, north-western Eyre Peninsula, South Australia. Kolballa Station was one of the first pastoral stations in the interior of the northern Peninsula and was based on water derived from the granite hill.

On a global scale, these granite upland-based conservation schemes are only minor but they are locally significant. Furthermore any saving of water, especially potable water, is admirable for water always has been, and remains, a vital commodity. It is the most precious of all our mineral resources and will become even more important. It has been estimated that by 2050 AD, the world's population will be of the order of 10 billion. Many will be short of water, for though there are about 14×10^{23} (1400 billion billion) litres of water on Earth, 97.5% of this is seawater and only 0.8% is potable and accessible. At the present time, every person on Earth uses on average one million litres every year, most of it for producing food or in manufacturing (*sensu lato*), but also, in the so-called developed world, for such labour-saving devices as dishwashers, washing machines and automatic car washers. There is still enough, on average, though some areas like central Asia, the Levant, and much of Africa, are already chronically short of water. But, with water use having tripled over the past half century, and doubling every 20 years, this will not be true for much longer. In those areas that are either overpopulated, or like most of Australia already short of water, there will be problems. Thus though water gathered and stored from granite outcrops may not loom large in the global water supply equation, every little source helps, and potential sources of water must not be recklessly destroyed. Even minor catchments like the granite bornhardts of the Wheatbelt of Western Australia and of northern Eyre Peninsula may become even more useful than they are and have been. Conservation must be encouraged and future needs borne in mind.

Recreation and tourism

Many granite outcrops stand high in the local topography and offer good views. Some have been sculptured into elegant, odd or just plain interesting shapes. Tafoni, with the opportunities they offer for games such as hide-and-seek, are irresistible to children. For these reasons, many granite hills are used for recreational purposes, either casually or in an organised fashion. Thus, many hills are used locally and informally for picnics, walks, runs and climbs; and though unspectacular this function cannot be overvalued for these sites provide invaluable space, interest and relaxation for many families and small communities.

On the other hand, many granite hills are tourist attractions, at various scales. Some provide excellent facilities and information, whereas others are good but low key. Hyden Rock generally, but Wave Rock in particular, is the prime example of intensive tourist activity (Twidale & Bourne 2000b). Facilities, including accommodation and food outlets, are excellent, and considerable trouble has been taken to encourage not only the casual camera-toting visitor but also those, increasing in number, who look for or are attracted by accurate information about what they are seeing and are willing to spend time exploring the area to improve their understanding. The information offerings are varied and include not only features of geological, and botanical interest but also something of the history and life of the district.

Murphy Haystacks, on north-western Eyre Peninsula, is an example of a low-key tourist site. These 'Haystacks' consist of granite pillars with flared sidewalls (Twidale & Campbell 1984; Fig 5) standing in a row on the crest of a hill just to the west of the main Port Lincoln-Streaky Bay road. They stand on what was Pat Murphy's property and it is said that the coachmen travelling the road would point out these haystack-shaped rocks to their passengers. They are unusual forms, with many minor features of interest, and to some eyes are aesthetically pleasing and reminiscent of some of Henry Moore's works. But they attract only a few visitors. Nevertheless, the notes displayed alongside the entry path simply, clearly and succinctly relate how the features originated. There is no shop selling drinks or souvenirs, and no

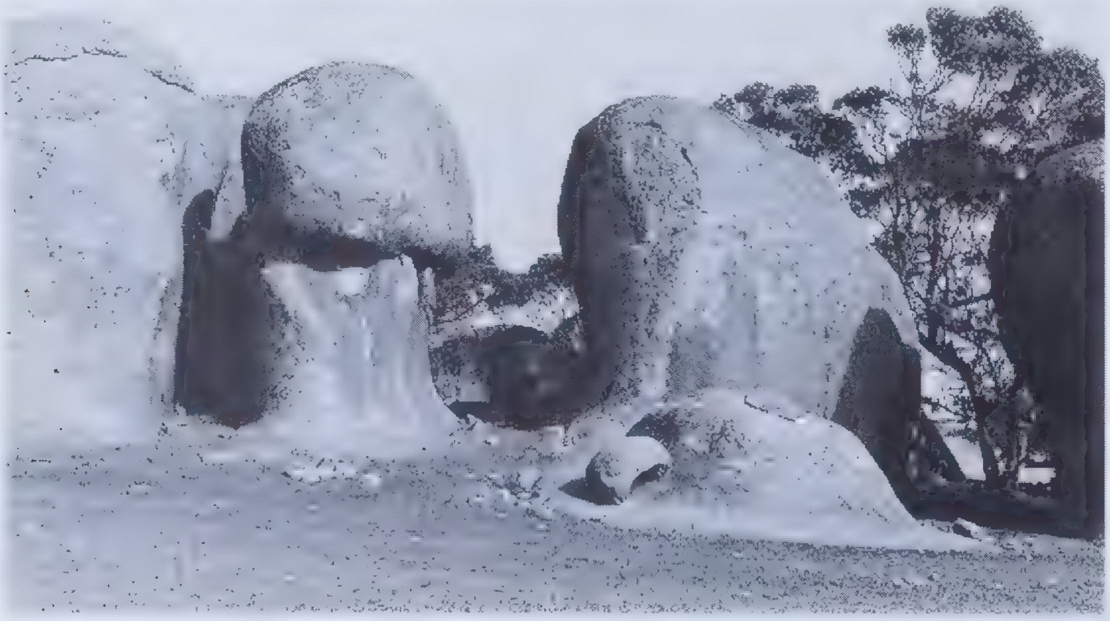

Figure 5. Part of Murphy Haystacks, a group of granite pillars between Streaky Bay and Port Kenny, north-western Eyre Peninsula.

charge for entry - just an honour box for donations for the upkeep of the facility.

Other sites are not so praiseworthy. Some authorities persist in propagating false information in order to sound the most (largest or smallest, highest or lowest, or whatever). For example, in addition to introducing conceptual errors, it is still claimed on official notices that Mt Wudinna (properly, Wudinna Hill) on north-western Eyre Peninsula is a monolith second in size only to Ayers Rock, whereas not only are there many higher and more extensive hills in various parts of Western Australia and in central Australia (*e.g.* The Granites, western Northern Territory, and the Everard Ranges in north-western South Australia), but Carappee Hill, only 120 km to the south-east of Wudinna is much higher and more extensive than Wudinna Hill. This error, and others which would be hilarious were they not so grossly and obviously inaccurate, is perpetrated and perpetuated despite accurate information having been provided to the body responsible for the notices. (A case of a good story overriding truth, a tendency which has shown up elsewhere). Moreover, some of the concepts mentioned are distorted or incorrect, and in some instances the presentation is ungrammatical. Considered altogether, such misinformation is worse than no information being offered.

Edutourism is another area of future development. Various restrictions concerning safety and entry to properties (and related legal obstacles) have made group education, whether at school, university or club level, difficult, and this together with the growth of such institutions as U3A (University of the Third Age, intended for adults with no formal or paper educational qualifications) will produce a growing demand for organised educational tours at specific, especially suitable, sites.

Conservation and management

Various demographic and social factors suggest that (eco)tourism and edutourism are industries of the future. If advantage is to be taken of this trend, then the granite outcrops must be prepared not only for use but also for preservation. Not only must accurate information be presented by way of literature and signage, but sites of special significance must be protected, as must vulnerable areas of the uplands. For example, false claims as to the local feature being the largest or smallest, oldest or youngest, have no place in advertisements; delicate features such as siliceous speleothems call for special protection, possibly by not being advertised; and patches of soil which are home to various plants need to be protected against trampling feet.

Building adjacent to granite hills ought to be controlled and again be subject to inquiry and permission from an impartial body. Outcrops destined for major tourist development need protection from humans. There is a choice of allowing visitors to wander at will, or to channel them into prescribed walks, although this dictates that some vulnerable areas may be trampled. In such areas, soil ought to be protected by slabs (of local rock), fencing and raised wooden decking. Even bare granite rock can be worn away in time and needs protection (in Galicia, north-western Spain, there are straight parallel gutters some 10-25 cm deep eroded in fresh granite due to the repeated passage of cart wheels, presumably iron shod). Visitors ought not to use footwear with metal studs or plates; rubber or plastic soles are preferable.

Tidiness ought to be encouraged (and time and money saved) by providing discreetly designed and placed rubbish containers. In addition it will be necessary to organise regular clean-ups to take account of the careless visitor.

Discussion

Nature and human interest, both aesthetic and scientific, have determined those outcrops that are of tourist, recreational or educational value and existing regulations and public opinion will presumably ensure that they will not be ravaged by quarrying in the foreseeable future. Similar but lesser concerns will limit the use made of such sites for water conservation; although such schemes need not be ugly and may indeed enhance the local landscape, for water (a reservoir) almost always adds to the attractiveness of scenery although diversion walls, fences and associated debris do not. One difficulty is that sites that are pleasant and interesting and locally useful for recreation, but carry or display nothing unique, may be endangered. Another is that significant features may not be recognised or appreciated at this time.

To help overcome these difficulties, it is suggested first that all major outcrops, and any others known to have features of interest, and any that are proposed for quarrying, ought to be surveyed, described and photographed (geology, landforms, flora, fauna, water potential and needs, historical significance). The survey techniques developed by the former CSIRO Land Research groups (*e.g.* Christian 1952) and classification and evaluation criteria evolved by various American agencies could be utilised (for a theoretical treatment of perceptions of landscape see *e.g.* Tuan 1974). The purpose would be first to record all that can be about the hills or outcrops, in case they eventually are destroyed, and second to form the basis of a register of outcrops. They could be then assessed and assigned a category according to perceived importance, with reasons given. Granite landforms are quite well understood (*e.g.* Twidale 1982a, Campbell 1997; Vidal Romani & Twidale 1998) but not all is known about them and there remain many debatable points. But whether understood or not, total morphology ought to be recorded. Possible utilisation could also be indicated in terms of such an evaluation.

Such a survey would allow the identification of sites that are of value for conservation or as sources of biological renewal, or that are of value for teaching purposes or which clearly demonstrate points of scientific argument and debate. Thus, Wave Rock is a superb example of a flared slope, and Yarwondutta Rock near Minnipa on north-western Eyre Peninsula is of scientific importance because of the spendid exposure of a concave weathering front which was naturally subterranean but which has been exposed by excavation in the interests of water conservation (Twidale 1962). In addition, the compact two metre exposure but complex regolithic profile exposed in a nearby quarry (Twidale 1986), and

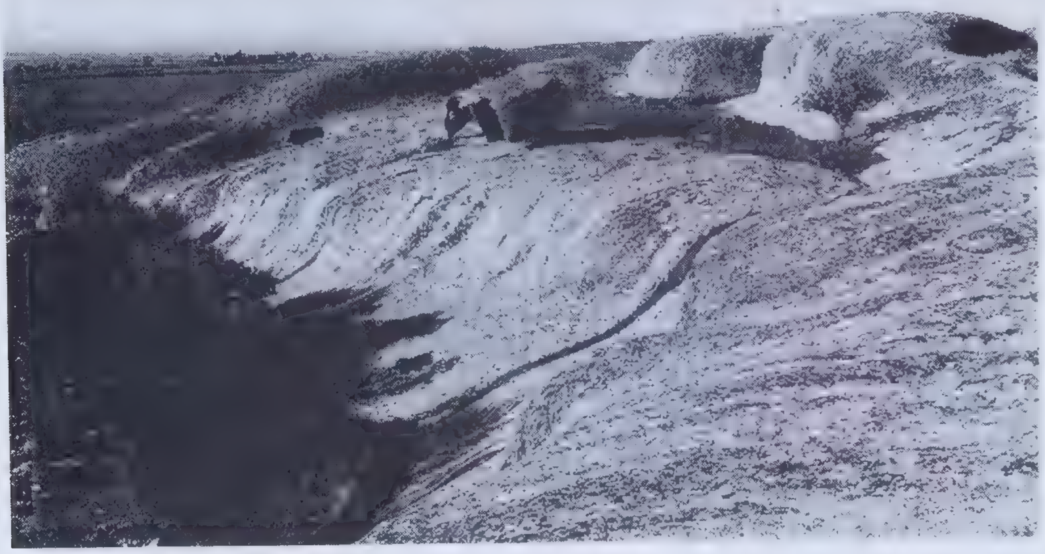

Figure 6. The stepped north-western slope of Yarwondutta Rock, Minnipa, north-western Eyre Peninsula. South Australia.

its overall stepped morphology (Fig 6) carries clear implications for general theories of bornhardt and of landscape evolution (Twidale & Bourne 1975; Twidale 1982b).

Granitic "islands in the bush" are subject to competing claims. In order to evaluate these claims in terms of particular sites it is suggested that an overall review and evaluation of major granite hills be undertaken to form the basis of optimal utilisation and conservation.

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Management implications of neotectonic activity at Minnipa Hill, north-western Eyre Peninsula, South Australia

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Abstract

An earth tremor which occurred on 19 January 1999 caused the development of a suite of small neotectonic landforms on Minnipa Hill, a low large-radius granite dome located near the town of Minnipa, on north-western Eyre Peninsula, South Australia. This event and its results carry several implications for the utilisation and management of such granite rocks, as well as being germane to the interpretation of several familiar landforms.

Keywords: granite outcrops, compressive stress, neotectonism, quarrying, hazards

Introduction

Minnipa Hill is one of several domical hills or bornhardts located in the Minnipa and Wudinna districts of north-western Eyre Peninsula, South Australia (Fig 1; Twidale 1964; Twidale & Campbell 1985). It consists of two separate exposures, locally referred to as the western and south-eastern rocks. Minnipa Hill South-east is an outcrop of massive impermeable granite exposed on the crest and eastern slope of the rise. In vertical section about 12 m of rock are exposed. It is delineated by prominent NW-SE and NE-SW trending fractures. Some of the lower slopes are flared.

The tremor and resultant forms

An earth tremor, estimated at about 2.3 on the Richter Scale, shook Minnipa Hill South-east in the late morning (1137 CDST) of 19 January 1999 (Twidale & Bourne 2000a). The tremor was shallow, so that most of the energy generated in the shake was dissipated at the surface. The quarrymen working at the site heard a loud bang just before the lunch break, and on investigating the hill upslope from the working area found the surface disturbed over an area about 170 x 120 m (Fig 2). The tremor caused several rock bursts, with the disruption of large blocks of granite (C2-C6 in Fig 2). For example, a block weighing some 730 kg was displaced 58-100 cm; a triangular slab weighing about 880 kg located low on the eastern slope was moved laterally up to 28 cm; one slab was displaced laterally leaving a quadrangular void some 20 x 90 x 25 cm. This movement was down a 4° slope and involved the displacement of slabs that in total weigh about 3330 kg. A block weighing some 110 kg jumped about 75 cm up a 7° slope (*cf* Ikeda 1996). In addition small fragments and flakes of rock were flung up to 25 m from the centre of the largest rock burst (C3 in Fig 2). Several low (up to 12 cm) fault scarps were formed, two of them in parallel and delineating a low amplitude horst. Huge flat-lying slices or wedges of rock were moved laterally (by 1-2 cm) relative to those below them. Two new A-tents were formed and widespread flaking of the rock was evidenced.

This was not the first earth tremor to affect the Hill, for evidence of at least two similar assemblages of superficially weathered and discoloured forms - flakes, displaced slabs, A-tents - are preserved at the site (C1 in Fig 2).

Management implications of the tremor

The Minnipa Hill bornhardt is typical of its type both in morphology and in origin. It is neither as extensive and high, nor as intricately sculptured, as are Ucontitchie and Wudinna hills, for example, but the component parts are typical of the many low "dimpled and grooved" (because of the development of numerous basins, or gnammas, and gutters or *Rillen*) domes that are exposed not only on north-western Eyre Peninsula but also in the Yilgarn, Pilbara and Salinaland divisions of Western Australia (see *e.g.* Jutson 1914). As to origin, most though not all bornhardts are upstanding because they are massive with few open fractures, so that water cannot readily penetrate and rot the rock. They are massive because they are in compression (Twidale 1964, 1982a,b; Vidal Romani & Twidale 1998; Twidale & Vidal Romani 1999). By contrast the granite of the plains is densely fractured so that water can penetrate and alter the granite. As far as is known, all the granitic bornhardts of Eyre Peninsula and the Wheatbelt area of Western Australia are of this type, and the recent development of A-tents, reverse fault scarps and slipped slabs shows that many have been and that some still manifestly are tectonically active (*e.g.* Twidale 1986; Twidale *et al.* 1991, 1993).

Granite hills possess different qualities but they are all subject to competing interests. In particular they are of potential value for quarrying, water conservation, tourism, local recreation, biological conservation and scientific research. In 1913, for example, Minnipa Hill was used as the catchment for a small water conservation scheme to supply water for the steam engines running on the then newly extended railway line from Port Lincoln (Twidale & Smith 1971). The eastern slopes of a small outcrop located some 200 m south of Minnipa Hill have been dammed and used for collecting water for stock. Minnipa Hill is the site of a microwave tower, because it

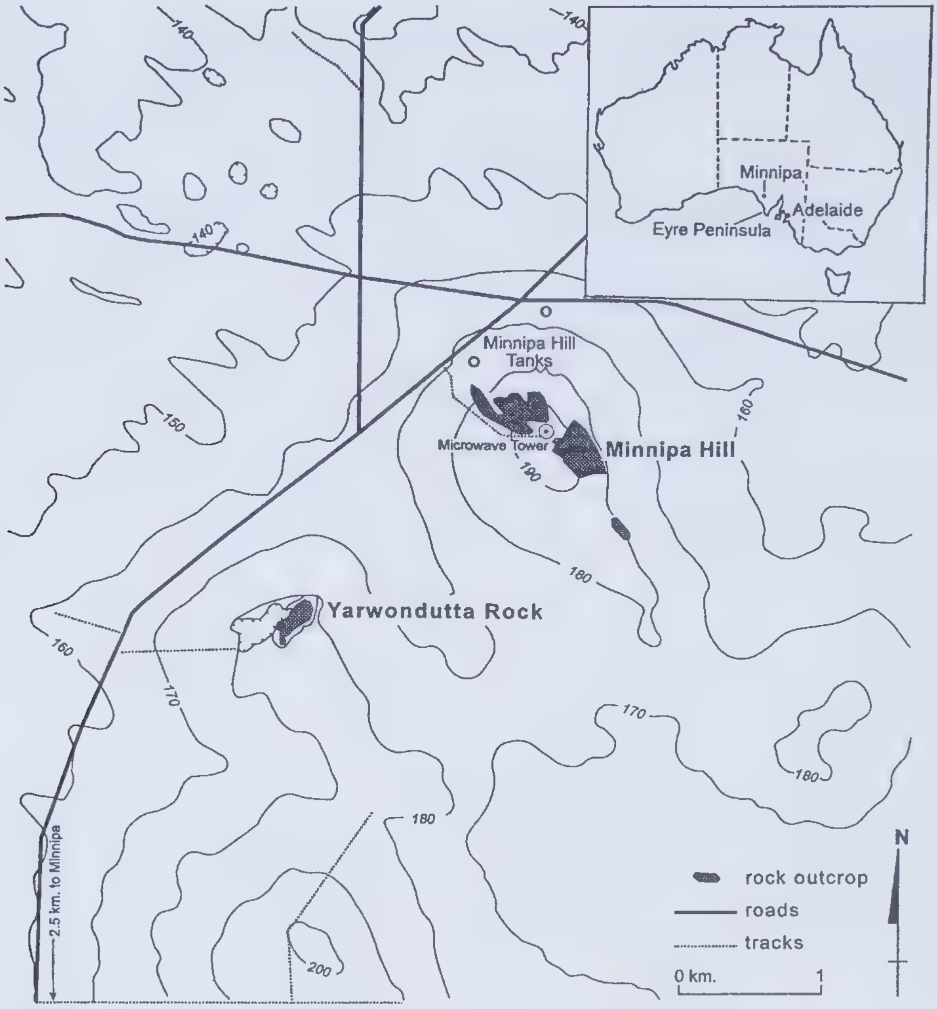

Figure 1. Location of Minnipa Hill, north-western Eyre Peninsula, South Australia.

is a local eminence, is geographically and legally accessible, and is not a recreation area. Quarrying for monumental stone began at the site in 1998.

Earth tremors such as that which affected Minnipa Hill on 19 January 1999 have implications for several of the possible uses to which granite hills are put. Prior to the tremor the quarrymen working the Minnipa Hill South-east quarry experienced operating difficulties. The rock adjacent to cut slots disintegrated to a depth of several centimetres, the bridges between drill holes (which became distorted) crumbled and there were minor rock bursts. All these are indicative of rock in compression. Quite apart from operating difficulties, rock bursts are dangerous to workers and anyone else who happens to be at the site at the time (see *e.g.* Isaacson 1957; Leeman 1962). The potential occurrence of rock bursts is also a cause for concern for tourist operators but the chances of them taking place where and when visitors are present at the sites is remote, and certainly less than other everyday hazards such as tripping, falling and breaking bones. On the other hand, displaced slabs at several sites (Little Wudinna Hill on north-western Eyre Peninsula, King Rocks and Hyden Rock in the Wheatbelt, The Granites near Mt Magnet in Salinaland) and fault scarps at King Rocks and Hyden Rock (Twidale *et al.* 1991; Twidale & Bourne 2000b), for example, show that earth tremors are not uncommon and that trails and paths for visitors ought not to be situated below perched slabs or boulders.

Albeit at a minor scale, the Minnipa Hill tectonic event also illustrates the possible problems posed by earth tremors for water conservation schemes. The floors and walls of several small rock basins (*e.g.* pan *in* Fig 2) were cracked and breached so that they no longer hold water. Sediment which had accumulated in the floors has been flushed away. Man-made structures, from dams to retaining walls, are similarly at risk.

Tectonic events like that evidenced at Minnipa Hill have the potential temporarily to disturb biological niches, for instance by causing arches and slabs to collapse and by rupturing the root systems of plants. Biological niches have been destroyed. On the other hand new ones were generated as slabs were arched and blocks pulled apart.

Such events are useful also in providing data relevant to various scientific controversies. Thus the event of 19 January 1999 at Minnipa Hill South-east is pertinent to the debates concerning the origin of bornhardts, sheet structure and A-tents (see *e.g.* Dale 1923; King 1949; Twidale & Sved 1978; Twidale 1980, 1982 a,b; Wallach *et al.* 1993; Twidale *et al.* 1996).

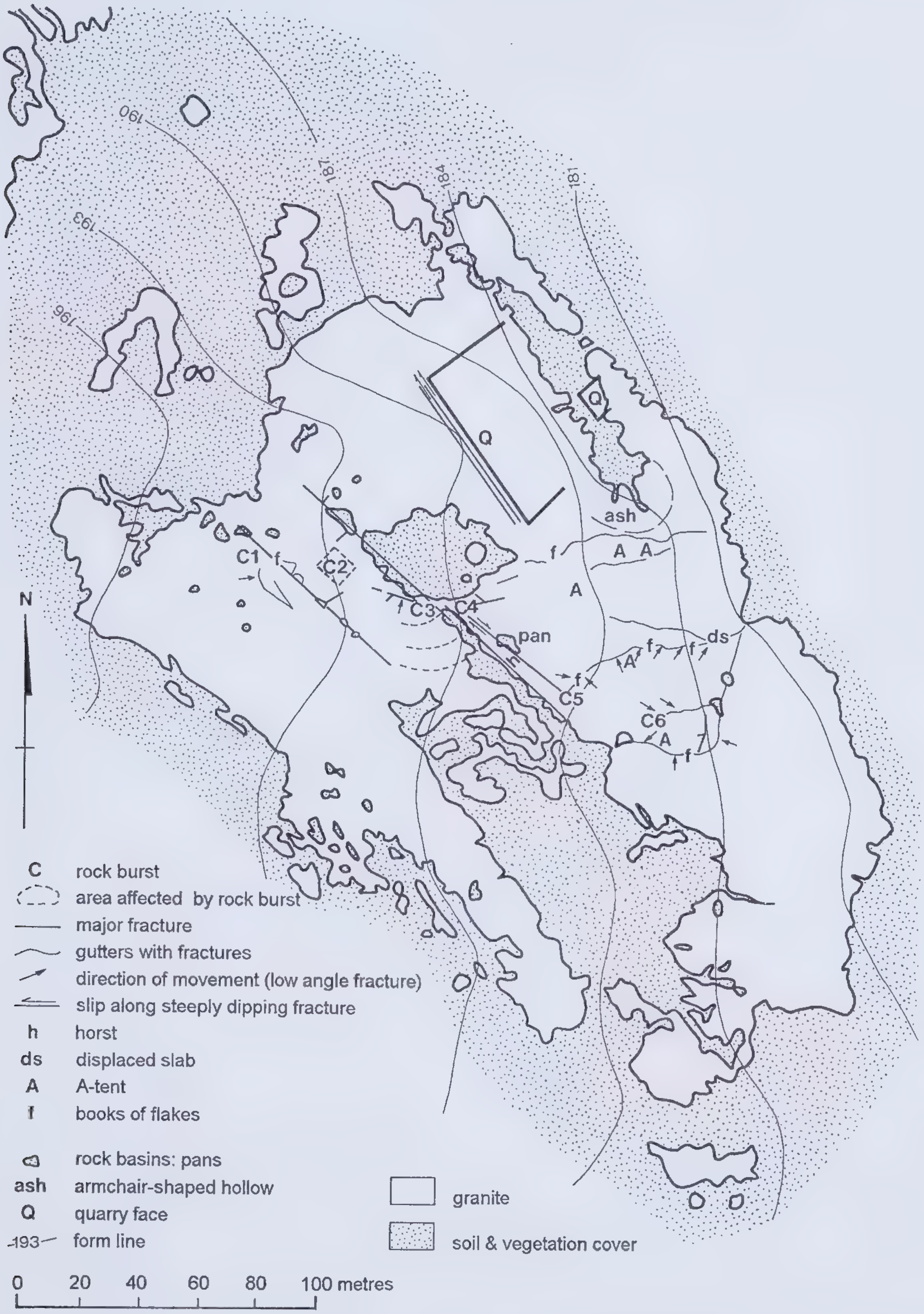

Figure 2. Map of Minnipa Hill South-east showing neotectonic forms resulting from the tremor of 19 January 1999.

Most granite hills are hills because they are in compression, are massive and are not penetrated by the water that is mainly responsible for rotting the bedrock and transforming it into a state in which it can be worn away. Both general theory and the site evidence show that granite hills are subject to disturbance by earthquakes and earth tremors, and mapping and analysis of the surface morphology show that their impacts have been experienced several times and hence are likely to recur in the future. Such possibilities ought to influence management plans, for the field evidence is clear.

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Cryptogams on granites

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Abstract

Cryptogams (lichens, fungi, mosses, liverworts and algae) are a vital part of the biodiversity of granite outcrops, yet are not well known. As with all groups of organisms, there are both common and rare species of cryptogams. Most cryptogams are vulnerable to disturbance, even human footprints. Proposals for research and conservation of cryptogams are presented.

Keywords: cryptogam, granite outcrop, mosses, liverworts, fungi, lichens, algae

Introduction

Cryptogams are small organisms that we tend to walk over and ignore, or not even see, as we traverse granite outcrops, or, for that matter, most habitats. Cryptogams are seldom so conspicuous as to excite great excitement. The name is from the Greek *cryptos* (covered, hidden) and *gamos* (marriage), in reference to the concealed nature of their sexual reproduction.

This paper is really a story of ignorance. My aim is not to present a highly scientific account of these fascinating organisms, or a mass of names and figures about them; rather it is to raise awareness of them. Indeed, there is probably no specialist in Australia, in any group of cryptogams, who could do so for the granite outcrops of south-western Australia. I shall return to this point, the almost total lack of researchers in cryptogams in this region.

First, I want to explain each group of cryptogams, then discuss research needs and conservation. You will see that we are at a very early stage in knowing what we have and how they live, probably equivalent to the knowledge of flowering plants a hundred or more years ago.

Cryptogams

Two groups of cryptogams are collectively called bryophytes; these are the mosses (which most of us at least recognise, even if we don't know their names) and the liverworts, which are much less conspicuous. Fungi are now considered to belong to one or more separate kingdoms, rather than included with plants. Lichens are intriguing mutual associations of fungi and algae or cyanobacteria. Algae, which include seaweeds and water blooms, also form large colonies on rock faces, on surrounding soil, or in pools.

Mosses

Mosses are small plants with separate generations, one the gametophyte (a leafy haploid phase, the commonly seen stage) and a diploid sporophyte that produces spores. The latter is relatively short-lived and less often noticed. Mosses have stems (usually with water-conducting strands) but no roots; rather they have root-like structures called rhizoids. Growth is from an apical cell. Sexual reproduction involves the production of male sperm cells in antheridia and eggs in archegonia. Following fertilisation, a sporophyte is formed, commonly on a stalk with a capsule at its apex. Here the haploid spores develop and are eventually released, controlled by a complex structure around the mouth of the capsule.

Perennial mosses survive desiccation by drying out, curling up and lying dormant until moisture improves. Ephemeral species have a short life span and survive as spores.

A moss, *Pleurophascum occidentale*, is the only cryptogam in the State that is Declared Rare Flora. A moss of uncertain classification as its fertile capsular stage has never been seen, it grows in exposed soil pockets at the edge of granite rock at Two Peoples Bay. Any change to its moisture regime will threaten its survival.

Liverworts

Most liverworts associated with granite rocks are on the soil aprons overlying or adjacent to rocks. They are thallose, most being more or less flat, close-pressed to the soil and attached to the substrate by rhizoids. A few are leafy and appear moss-like. Reproduction is commonly vegetative, by means of break up of a thallus, or production of groups of cells called gemmae that break away and develop into new plants. Like mosses, liverworts are poikilohydric *i.e.* they are resurrection plants with the ability to become dormant in unfavourable conditions (usually lack of moisture) but resume growth when conditions improve. In contrast to mosses they lack stomata and have no specialised conducting tissue.

Fungi

Fungi are now considered to belong to one or more separate kingdoms, rather than included with plants. They lack chlorophyll, have no vascular system, and reproduce by spores. The larger (or macro-) fungi include forms well-known to all as mushrooms and toadstools, cup fungi and stinkhorns. That part of a fungus is its fruiting body and is the only part readily visible. The 'vegetative' part is a mass of slender threads known as mycelium, usually hidden in soil, on rotting wood, plant stems or leaves etc. The fruiting bodies are not produced every year, hence years of survey are required if a complete inventory of even larger fungi is to be obtained.

The microscopic fungi are scarcely known. It is estimated that there may be as many as 250 000 species of fungi in Australia; only some 5% are currently known.

Fungi are absolutely crucial to the survival and well-being of all other life on earth. It is said that other groups of organisms could disappear and other life would continue, but if the fungi were to go then life as we know it would also disappear. They provide us with food and pathogens, they include yeasts, and they are widely involved in decomposition.

Lichens

Lichens are intriguing mutual associations of fungi and algae or cyanobacteria. For nomenclatural purposes they are classed as fungi, but researchers tend to specialise in lichens or fungi. Having an algal component with chlorophyll they are able to manufacture their own food. Presumably the fungus obtains carbohydrates from the alga, and in return the alga receives nutrients absorbed from the substrate and protection. The cup-like fruiting bodies that we see represent only the fungal component, which grows and reproduces just as an ascomycete fungus. As far as I know, no-one has yet discovered how the algal component reproduces, nor how the alga and fungus come together to form a new lichen plant.

Lichens grow on soil, rock surfaces, bark and sometimes leaves, though the latter not in Western Australia as far as I am aware. Those on otherwise bare granite rocks tend to escape fire as there is no adequate fuel to carry fire across them, but I have seen one instance (Wattengutten Hill) of an extremely hot summer fire on a strong wind scorching all lichens from the surface. I have never had the opportunity to return to the site to see what recolonisation has occurred.

As an indication of our poor knowledge I would cite two species (*Neofuscelia subbarbatica*, *Xanthoparmelia nana*) each known from one granite rock in the hills east of Perth, and two (*Paraparmelia sammyi*, *Paraparmelia sargentii*) known only from Yillimining Rock east of Narrogin. Indeed, Yilliminning Rock is the only rock for which even a preliminary list of cryptogams is available, and that of lichens only (33 species, Piggott & Sage 1997).

Either these species are more widespread, or there are likely to be many more species of very restricted range out there awaiting discovery and classification.

Algae

Probably everyone knows some algae, if not by that term. They include seaweeds and water blooms (an odd term, given that they do not have flowers), and if you have ever slipped on a rock in a stream or a damp path the odds are that algal growth caused the slipperiness. They also include diatoms, desmids and other phytoplankton, microscopic algae that are the basis of the food chain. It has been said that without algae, all bodies of freshwater would effectively be dead. We tend not to associate algae with granite rocks or with the soil surface. Those of granite rocks are very small but may form large colonies on rock faces, on surrounding soil, or in pools.

One of the most recent publications on freshwater algae in Australia (Entwistle *et al.* 1997) states, very bluntly, that those on rocks have been 'little studied in Australia' and on soil are 'largely unknown'. It is an indictment of our failure to study them in this State that this recent reference includes very few records from here. They are important in colonising soil and rocks after extreme disturbance such as fire, though we have no data on how they do this. They stabilise loose soil, provide food and, in pools, shelter.

Chara and *Nitella* are two genera of algae with a readily recognisable plant form that occur on pools and slow-flowing streams.

Conservation

A goal of the 'National strategy for the Conservation of Australia's Biodiversity' is the protection of that biodiversity and the maintenance of ecological processes and systems; yet the resources to discover huge sections of that biodiversity have still not been made available. In Western Australia, the 'Wildlife Protection Act' at least has been amended so as to specifically cover cryptogams as well as vascular plants; but so far only the moss *Pleurophascum occidentale* is declared as rare, while two fungi, twenty-one lichens and three other mosses are listed as Poorly Known. I suspect these numbers should be much larger. All other cryptogams therefore are incidentally conserved when they occur in areas reserved for other organisms or purposes. In the short term, until we learn more about them, habitat conservation is the only way to go, but without inventories of what is present we have no way of knowing what percentage of cryptogams we are preserving in this way.

From left to right: Peak Charles, a high granitic dome (650 m) in a semi-arid zone, with bands of a freshwater alga; Bands of a freshwater alga on Mt Churchman, a large granitic rock in an arid zone; Mosses (*Campylopus*, *Brutelia*) and lichen on Shannon Rock, a granitic slope in a high-rainfall zone; Moss (*Grimmia*) in its dormant state on Billyacatting Hill, a low granitic dome in a semi-arid zone; The lichen *Siphula coriacea* among mosses and sundews (*Drosera*). Photographs by AS George

As George Scott has written, 'estimates of rarity are, with some exceptions, merely confession of ignorance' (Scott *et al.* 1997). That ignorance covers taxonomic knowledge, classifications for rarity that are inadequate for cryptogams (it is virtually impossible to count individual plants of bryophytes, lichens and many fungi, hence another measure of abundance is required), and understanding of the organisms (for example, just because a fungus does not produce a fruiting body does not mean that it is not there).

Management

Because cryptogams are small and commonly fragile they are susceptible in the extreme to physical disturbance. Even soft-soled shoes can damage them, and anything heavier such as vehicle tires can obliterate them. And we have no idea how these organisms respond to fire. The retaining walls already built on a number of rocks for water catchment would have changed the water regime both immediately above the wall and downslope of it, resulting in changes that we can only guess at because of our ignorance. There would also be a change in light intensity in the microhabitats along the 'down-sun' side of such walls. They can also be highly sensitive to atmospheric pollution such as vehicle and industrial exhaust fumes.

Recommendations

I can hardly do more than repeat those of Scott *et al.* (1997):

1. The most urgent need is skilled workers. The Western Australian Herbarium (Department of Conservation and Land Management) has never had any staff specialising in these groups. There is a small collection, mainly of lichens and mosses, currently maintained by a volunteer. Many species recorded for the State are unrepresented in the collection. The only systematic work is by specialists in other States and overseas.

   In Western Australia, we have no lichenologist, no bryologist, no freshwater phycologist except on those of economic importance and Jacob Johns, Curtin University (on diatoms). We have one mycologist studying macrofungi, and several on species important in silviculture and agriculture.

   In a submission to the latest 'State of the Environment' report I drew attention to the need to increase the taxonomic effort on cryptogams. The response was to agree but refer it to the relevant agency, presumably the Western Australian Herbarium. To my suggestion that specialist cryptogamic botanists be appointed the response was even weaker—'this is beyond the scope of this report.' I suspect this means that there will be no change to the current zero level of research.

2. A second, vital need is adequate collections on which a sound taxonomy can be established. This will tell us what we have and how it relates to the rest of the country and the world (many of these organisms are far more widespread than are our flowering plants).

3. Next, we need geographical and ecological data so that we can learn where and how to conserve them, whether more reserves are needed.

4. A comprehensive database with national and international links should be established. This is especially important given that a number of species recorded for the State are not represented in our collections.

5. Public awareness of crytogams should be raised through publications, lectures, posters, resource kits for schools etc.

6. Land managers should be trained so that they may be aware of cryptogams, their nature and their needs.

7. Research should be undertaken into potentially useful cryptogams.

8. Throughout Australia, appropriate, uniform legislation should be set up for protection of crytpogams.

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The invasibility of tropical granite outcrops ('inselbergs') by exotic weeds

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Abstract

Granitic and gneissic rock outcrops ('inselbergs') that rise abruptly from surrounding plains are of widespread occurrence on old crystalline shields. In the tropics this geologically old ecosystem occurs throughout a broad spectrum of vegetational and climatic zones. Inselbergs usually bear a vegetation that is drastically different from those of the surroundings due to their edaphic and microclimatic aridity. Because of their low agricultural potential, tropical inselbergs form in many regions the last refuges of natural vegetation types. However, there is increasing evidence for non-native weeds getting established within inselberg plant communities by using roadsides and fallow land as stepping stones. In both Africa and South America, exotic weeds have become a severe danger for indigenous plant communities on rock outcrops because of their high competitive ability. A survey is provided about the most important weeds on tropical inselbergs which shows that intentionally-introduced species, like *Ananas comosus* in West Africa, cause the most serious problems. Moreover, different rock outcrop habitats are analysed in regard to their invasibility.

Keywords: conservation, disturbance, endemics, fragmentation, inselbergs, weeds

Introduction

More or less dome-shaped granitic or gneissic rock outcrops are called inselbergs when they rise abruptly from the surrounding plains. They form geologically and geomorphologically old landscape elements that are often more than 50 million years old (Bremer & Jennings 1978). Throughout the tropics, subtropics and temperate regions they are widespread on the old crystalline shields where they form conspicuous landmarks (Plates 1 & 2). Environmental conditions on inselbergs are severe due to high insulation and evaporation rates, and because of the lack of a continuous soil cover this explains their large degree of floristic distinctiveness. The harsh growth conditions on inselbergs have led to the development of specific adaptive traits. Of particular importance in this respect are desiccation-tolerant vascular plants for which inselbergs are among the most important growth sites (Porembski & Barthlott 2000). Certain floristic regions harbor an inselberg vegetation rich in endemic plants, such as Madagascar or the Brazilian Atlantic rainforest, with numerous species being known to occur in only a few localities.

For a long time, the vegetation of inselbergs was denoted as lithophytic without further differentiating between individual habitats. Today, however, it is evident that inselbergs form ecosystems that, despite large differences in regional floristic composition, comprise clearly circumscribed plant communities (Porembski *et al.* 2000). Cryptogamic crusts, monocotyledonous mats, shallow soil-filled depressions, seasonally water-filled rock pools and ephemeral flush vegetation are particularly characteristic among those communities which occur under open, fully-exposed conditions on rock outcrops.

Over the last decades, a considerable number of studies devoted to the knowledge of the vegetation and ecology of both temperate and tropical inselbergs have been published (for reviews see Porembski *et al.* 1997; Barthlott & Porembski 1998). Because of their low agricultural potential and sometimes difficult access, inselbergs form in many regions the last refuges of natural vegetation types (Plates 3 & 4). However, it has already been noted (Wyatt & Allison 2000; Porembski *et al.* 1998) that under certain circumstances inselbergs may lose their island-like refugial character with severe consequences to their often highly unique vegetation. In many tropical and subtropical ecosystems, alien plants are the biggest single threat to plant conservation (Crawley 1997) and in certain regions introduced plants have become a problem on inselbergs too. It is the aim of this paper to provide a short overview of the threats to the vegetation of inselbergs in general and of the causes of plant invasions within this ecosystem.

Alien plants on tropical inselbergs

Due to the open character of their vegetation cover and because of frequent climatic disturbances, inselbergs are susceptible to new colonists. Today, however, apart from native plant species, exotic weeds that are good dispersers invade from adjacent disturbance-prone sites (*e.g.* roads, pastures). The importance of introduced species on inselbergs in temperate regions has been discussed concisely by Ornduff (1987), Hopper *et al.* (1997) and Wyatt (1997). In particular inselbergs in Western Australia bear a large number of introduced annual weeds which may comprise more than 20% of the whole outcrop flora (for details see Ornduff 1987 and Ohlemüller 1997). According to Wyatt (1997) weedy species on granite outcrops in the south-eastern United States have once been endemics restricted to this ecosystem. Moreover, it can be assumed that granite outcrops obviously have played a role as evolutionary springboard for certain present-day widespread weeds in the Piedmont region.

In the following, regional accounts of alien plants on tropical inselbergs are presented. The data given are mainly based on experience in the field obtained over the last decade in different tropical regions but otherwise published information was also considered. The alien weeds that are mentioned here represent non-indigenous plant species that were introduced intentionally or unintentionally and thereafter became established in considerable quantities. Individual sightings of non-indigenous plants on inselbergs are not included. Since data about Asian inselbergs are almost non-existent, the focus will be on African and South American inselbergs.

Africa, Madagascar, Seychelles

The vegetation of African inselbergs shows considerable regional differences in floristic composition and species richness (for review see Barthlott & Porembski 1998). Granitic and gneissic inselbergs are found in all vegetational and climatic zones of Africa. They occur over a broad range of primary and secondary plant formations and are frequently associated with religious purposes that have given them in certain regions a protective status. The most serious dangers to this ecosystem are deliberately lit fires, quarrying, to a lesser extent cattle grazing (Plate 5) and subsequently the arrival and establishment of non-native plants.

Since inselbergs in the Ivory Coast have been most thoroughly investigated hitherto within Africa, I concentrate in the following account on this country. Like most parts of West Africa, the Ivory Coast is characterized by a rapid conversion of primary forests into plantations, various stages of forest regrowth and fallow land. Over the last decades the speed and extent of landscape fragmentation has reached massive proportions. Inselbergs situated in rainforest are ecologically highly-isolated, sharing almost no species with their surroundings. Today outcrops situated in the Ivorian rainforest region have successfully been invaded by introduced weeds (Porembski *et al.* 1996) that probably have used roadsides and other open sites as ways of access. Most prominent invaders are certain South American grasses *e.g. Axonopus compressus* and *Panicum laxum* that preferentially can be found in shallow soil-filled depressions and rock fissures. With regard to invasibility, shallow soil-filled depressions, crevices and rock pools are colonized preferentially by alien plants. Far less threatened by invading alien species are monocotyledonous mats and ephemeral flush vegetation.

Inselbergs occurring in the neighbourhood of villages and near pineapple plantations occasionally became infested by the bromeliad *Ananas comosus* that is able to colonize a broad range of habitats. When established (frequently due to dispersal by humans) on inselbergs in humid parts of West Africa, this South American species becomes highly competitive. Preliminary observations indicate that *Ananas comosus* is a strong competitor to the indigenous mat-forming Cyperaceae *Afrotrilepis pilosa*. At certain localities in the Ivory Coast *Afrotrilepis pilosa* has already succumbed to *Ananas comosus* which there is now the dominant mat-forming species (Plate 6).

Similar to the situation in the south-eastern USA, Ivorian inselbergs act as an evolutionary springboard for weedy species. Most of all short-lived species that are typical for exposed habitats on outcrops are nowadays widespread colonisers along roadsides and other ruderal sites. The Commelinaceae *Cyanotis lanata* is the most prominent representative of these inselberg escapees. This species preferentially colonizes stony road banks where it forms dense stands, like its natural growth sites on rock outcrops. Other inselberg escapees belong mainly to the Poaceae (*e.g. Sporobolus* spp) and Cyperaceae (*e.g. Fimbristylis* spp) which likewise colonize roadsides and open ground. At the moment, however, it is difficult to predict whether these taxa will in the long run become successfully established members of ruderal plant communities.

The Madagascan rock outcrop flora is well known for its high percentage of endemics. In particular, granitic and gneissic outcrops on the Plateau Central are famous as a 'succulent paradise' (Rauh 1995). In certain areas of Madagascar the neotropical *Agave sisalana* which is cultivated for fibre has invaded inselbergs where it has become a serious threat to the indigenous vegetation. Due to its large size and rapid propagation, it must be feared that *Agave sisalana* has the potential for out-competing numerous native outcrop species in Madagascar.

On the granitic islands of the Seychelles, granitic outcrops are occasionally colonized by alien plants. Species like *Cinnamomum verum* and *Alstonia macrophylla* are among the most important alien species (Fleischmann *et al.* 1996). However, it seems that these inselbergs are not yet seriously endangered by invasive plants because of extremely high degrees of native regeneration. Moreover, the aridity of this ecosystem and the low fertility of the soils limits the probability for the establishment of these mesic invaders.

South America

As in Africa, inselbergs occur over a broad range of South American vegetational and climatic zones. The threats to their frequently highly diverse flora are the same as in other tropical regions. More pronounced, however, are disturbance effects caused by tourists and rock climbers in certain regions. Inselbergs in the Brazilian Atlantic rainforest (*e.g.* the famous Pão de Açucar of Rio de Janeiro) are particularly prone to these anthropogenic pressures and are in the focus of the following considerations.

Deforestation and landscape fragmentation have caused the near disappearance of the Atlantic rainforest, leaving only *ca* 4% of its original extension. Rock outcrops situated in this region are exceptionally diverse and rich in endemics (Porembski *et al.* 1998). However, because of the deforestation these outcrops have lost their island-like attributes (*e.g.* their isolation). This enabled a certain number of exotic weeds to successfully invade inselbergs via roads and other ruderal sites. Of major importance in this respect are neophytic grasses (*Melinis repens, M. minutiflora, Panicum maximum*) that today are found throughout south-eastern Brazil on nearly all inselbergs. The two species of *Melinis* occur in dense populations and colonize with preference clefts and fissures and sites that showed signs of human disturbance (Meirelles *et al.* 1999). During rainless periods the then dry grasses

Plate 1. Rock outcrops like inselbergs attract much tourism interest, as is the case with the famous Pão de Açucar of Rio de Janeiro which is accessible by cable car. Situated within a large city, the Sugar Loaf still bears much of its typical vegetation.

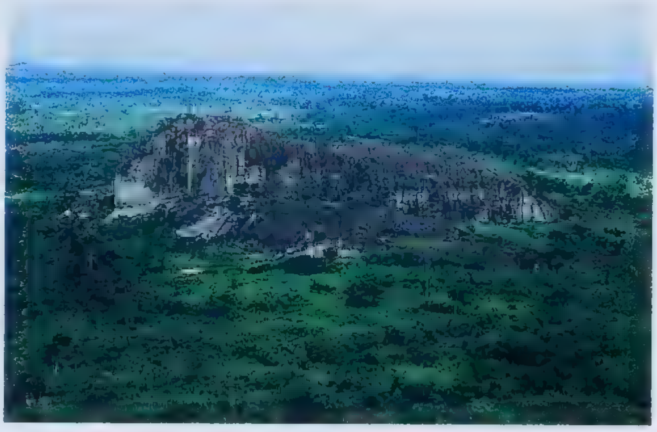

Plate 4. Over much of West Africa the rainforest has disappeared. Today a mosaic of different forest succession types and agricultural land forms the typical surroundings of inselbergs.

Plate 2. Stone Mountain in Georgia is the largest granite outcrop in the United States. A cable car brings thousands of visitors each year to the summit of the mountain, which causes considerable damage to the unique plant communities.

Plate 5. Cattle grazing has become a serious threat to the vegetation of inselbergs in most parts of the tropics.

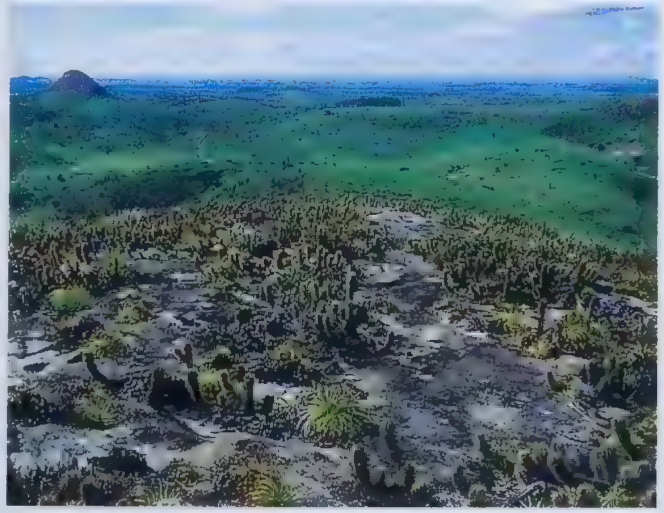

Plate 3. Inselbergs surrounded by pastures form the last refugia of natural vegetation within eastern Brazil where the Atlantic rainforest has largely been destroyed.

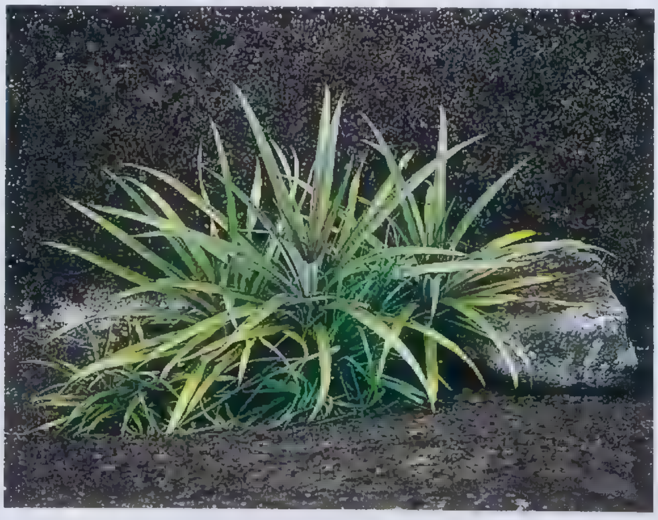

Plate 6. The invading bromeliad *Ananas comosus* has become a serious threat to native plants on inselbergs in the humid parts of West Africa.

enhance the risk of fire considerably. Near human settlements and depending on the extent of anthropogenic disturbance, further neophytes can be observed. Fairly frequent are leaf succulent species of the genera *Kalanchoe* and *Aloe* that sometimes occur as dominants on inselbergs. Preferred habitats of these introduced weeds which mainly escaped from gardens are crevices and monocotyledonous mats.

Inselbergs as potential sources of future weeds

As could be demonstrated in the south-eastern USA (Wyatt 1997), granitic outcrops in the tropics too may act as an evolutionary springboard for weedy plants. With deforestation and landscape fragmentation still advancing one can predict that the number of weedy escapees from inselbergs will increase. Most of all short-lived species on inselbergs with effective modes of dispersal represent suitable candidates that have the potential of becoming future weeds. In being adapted to cope with frequent disturbances these species already possess many key adaptive traits for a successful career as a ruderal plant. In contrast to this, it can be ruled out that strict inselberg specialists such as slow growing desiccation-tolerant vascular plants are of any importance in this respect. In West Africa some indigenous elements (*e.g. Cyanotis lanata, Dissotis rotundifolia*) of the widespread weed flora probably have been originally restricted to azonal habitat patches, such as granite outcrops. Other potential weeds from West African inselbergs are contained within the Poaceae and Cyperaceae that are richly represented within shallow soil-filled depressions and rock fissures. As the number of annuals on South American inselbergs is much lower their importance as sources of future weeds is considerably lower. However, it is remarkable that a number of local inselberg endemics is closely related to widespread ruderals. It is not clear, however, whether these endemics really have acted as sources of ruderal species.

Conclusions and recommendations

The widespread opinion of rock outcrops as possessing no value for agricultural purposes and their religious importance had protected them over long periods. As has been shown above, alien plants are today a potential threat to the unique vegetation of inselbergs in different tropical regions. With increasing habitat destruction in the surroundings of rock outcrops, it can be expected that this ecosystem will become in the future more exposed to the invasion and establishment of exotic weeds. This could have serious consequences for the regeneration and long-term survival of many endemic species whose competitive ability is relatively low. On both South American and African inselbergs, the invasibility by alien plants is enhanced by human activities (*e.g.* fire, off-road driving) that destroy the natural vegetation cover and thus provide open, disturbed establishment sites. In particular, near plantations and villages inselbergs became in certain regions infested by exotics to such a large extent that an eradication of the alien plants is no longer possible without considerable effort. Scenarios like this are only to be avoided if damage to the vegetation of inselbergs is kept to a minimum. Up to now, inselbergs have only accidentally been included in conservation measures (Meirelles *et al.* 1999). Due to their highly unique ecological character they form local biodiversity hot spots and refugia of eminent importance for both flora and fauna. Granite outcrops therefore should be consequently integrated within management plans for nature conservation and particular priority should be given to outcrops situated within biodiversity hot spot regions.

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Environmental weeds and granite outcrops: possible solutions in the "too hard basket"?

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Abstract

Granite outcrops and the myriad plant communities found associated with them are particularly vulnerable to weed invasion. Undesirable impacts can result from many species or just one aggressive invasive species. Suggestions for weed planning and management are made in relation to granite outcrops, but knowledge gaps are discussed as well.

Keywords: environmental weeds, biotic threat, threatened flora, granite outcrops

Introduction

Weeds are a major threat to the conservation of biodiversity in Australia, at species and ecosystem levels (Adair 1995). Known impacts for ecosystem function include competition for resources, prevention of recruitment, and altered fire regimes (Csurhes & Edwards 1998). Weed invasions are known to alter vegetation structure (Bridgewater & Backshall 1981) and have been implicated in the extinction of threatened species (Leigh & Briggs 1992).

Granite outcrops have unique features such as 'rock meadows' and crevices, which have high levels of floristic richness and endemism (Hopper *et al.*, 1997). Soils in these environments as well as around the base of outcrops often have seasonally high moisture levels. Combined with possible exposure to fertilizer drift and disturbance from fire or recreational activities, these habitats are likely to be highly vulnerable to opportunistic invasions from introduced plant propagules (Pigott & Sage 1997).

Studies of flora on granite outcrops in south-west WA have reported high numbers of exotic species (Hopper *et al.* 1997; Hussey 1993). Another granite outcrop study found a lower than expected proportion of weeds but the negative impacts of a few serious species (Pigott & Sage 1997). Increased proportions of weeds in relation to native species as well as evidence of aggressive species are alarming as both situations ultimately lead to breakdown of plant communities.

Types of weeds

Some 54 exotic plants (presumed naturalized) have been recorded as associated with granitic habitats and soil types in WA (Anon 1998). The true number is likely to be higher as many weed invasions remain unvouchered (Pigott 1999), existing specimen labels lack sufficient details, or the habitat association has not been databased. Weeds worth noting here include *Asparagus asparagoides*, a Weed of National Significance (Thorp 1999), *Watsonia meriana* var *bulbillifera*, recorded in granite outcrops at Helena Valley (Hussey 1993), *Juncus bufonius* and *Casuarina cunninghammiana* subsp *cunninghammiana*, examples of herbaceous and woody weeds with high potential invasiveness and impact. For example many of the cosmopolitan weeds collected at Yilliminning Rock in south-west WA (Pigott & Sage 1997) are not included above. Some of the weeds recorded were *Aira careophyllaceae, Briza maxima, B. minima, Hypochoeris glabra, Romulea rosea* var *australis* and *Ursinia anthemoides*.

As in this study, weeds recorded for granite outcrops and surrounding vegetation are mostly annual species *e.g.* Poaceae (Hopper *et al.* 1997) or those with annual emergent cycle, such as the Iridaceae family (Hussey 1993). These plants are able to respond rapidly to changing environments through spread of wind-borne seed or underground reproductive parts. Spread of weeds by rabbits is common, introducing quite noxious species such as cape weed (*Arctotheca calendula*) to disturbed areas adjacent to healthy bushland (Hussey 1998).

Examples of weed threats

For south-western Western Australia, some 5 species of threatened flora associated with granite habitats are recorded as threatened by environmental weeds (Brown *et al.* 1998; Sage & Pigott 1999). These are *Caladenia caesarea* subsp *maritima* ms, *Darwinia acerosa* and *Villarsia calthifolia* (all declared Rare), *Caladenia integra* (Priority 4) and *Goodenia drummondii* subsp *megaphila* (Priority 3). All are threatened by annual herbaceous weeds (unpublished data). An example of a woody weed affecting biodiversity conservation in granite outcrops is known from Victoria. Boneseed (*Chrysanthemoides monilifera* spp *monilifera*), another Weed of National Significance, is threatening populations of *Pterostylis truncata* at the You Yangs Regional Park, near Melbourne, Victoria (Miller & Eales 1999).

Rapidly spreading and aggressive environmental weeds threaten other special plants, such as the granite endemic *Pimelea graniticola* (formerly a P4). In this example *Freesia alba* x *leichtlinii* is altering the structure and potentially the composition of several plant communities at Yilliminning Rock in WA's wheatbelt (Pigott & Sage 1997).

To date there are no reports of endangered plant communities directly threatened by environmental weeds. This could largely be due to reporting and the relatively low numbers of vegetation studies on granite outcrops in the region. However for Victoria, rock outcrop vegetation (including granite) is threatened by 26 serious weeds (about 25% of local weeds) (Carr *et al.* 1992).

Weed management planning

Weed management in granite outcrops is no different to weed management in other types of remnant vegetation. Identification and mapping of priority weeds is an important first step in the overall planning process (Brown 2000). Site-specific information on native plant communities, threatened flora and other special issues is essential. A grid system can be used to plot populations of weed species and other important information (Brown 2000). These maps can then be used by whoever carries out the control work, *e.g.* community group or local government workers. Choice of control methods is important as resources in local government and community groups are limited. Monitoring is also critical, particularly where eradication of a weed is the desired result (Brown *et al.* 1999). Weed management plans should relate or be integrated with management or rehabilitation plans for a remnant.

However, it is also important to consider the source of the weed and the likely impacts of any control work. Other weeds are also likely to invade, taking advantage of disturbance activity associated with the removal of primary target weeds. For degraded granite outcrops, intensive management should include fencing off stock, fire management and direct seeding of appropriate native species. Some excellent case studies are provided by Hussey (1998), listing steps to take for particular situations.

Weed management techniques

The most difficult and controversial topic of remnant bushland management is undoubtedly weed control techniques. Is herbicide use appropriate at a particular site? If so, what products, rates and time of application will work best? These questions are intrinsically more difficult to answer than in an agricultural situation (Ainsworth 2000). In a crop or pasture the aim is to kill weeds whilst leaving a single crop species or a few pasture species relatively unaffected. By contrast in natural ecosystems the aim is to kill weeds whilst having no adverse effect on a wide range of different native species. Not only is the problem harder but herbicide use on most environmental weeds is commercially insignificant and therefore companies have no financial incentive to do the appropriate research. The most successful herbicides in use are those that selectively affect grasses, rather than those with a broad spectrum.

Pulling individual plants of serious environmental weeds can result in successful long-term control and improve recruitment of native species (Kirkpatrick 1986). Community groups can successfully apply techniques of pulling or killing individual weeds with a spot application of herbicide after careful planning. This practice could be applied to weed management on granite outcrops such as removal of *Freesia alba* x *leichtlinii* at Yilliminning Rock.

Conclusions

Weeds are certainly a threat to the conservation of the unique biodiversity of granite outcrop communities. As for other specialized habitats, weeds are poorly recorded and collected for granite outcrops in WA, and particularly with respect to threatened species and communities. Careful planning can assist in removal of serious weeds and also play an important role in the management of key granite outcrop reserves. Some manual and chemical techniques are already available but there is a large knowledge gap in this subject. As in all areas of Landcare today, community groups have an important role to play in the conservation and management of granite outcrops. However resources for research into the ecology and management of environmental weeds in Australia are low and do not meet higher community expectations. It may be another example where weed science is in the "too hard basket".

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Habitat template for invertebrates on granite outcrops

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Abstract

This study considers the known occurrences of invertebrate taxa from granite outcrops of southern Western Australia. The microhabitats occupied are briefly described. A schematic habitat template for composite outcrop configurations is presented. Only "ground" living or those directly associated with rock surfaces and aquatic taxa are considered. Rock flakes (exfoliated slabs) and rock pools have the richest taxonomic representation. These habitats, and moss swards, are also the most vulnerable to human induced disturbance. Seepages, from certain moss beds and meadows are important for retaining relictual taxa. The anomaly of confinement to isolated rocks of geographically widespread species is posed. Conversely, certain ancient genera are believed to have speciated around rocks following isolation associated with onset of arid conditions in the surrounding landscape.

Keywords: granite outcrops, climatic change, endemicity, species inventory, microhabitat, water capture, conservation

Introduction

Granite outcrops are salient features across south-western Australia from the Darling Scarp eastward to Eyre Peninsula. Within this broad geographic area, the southern part of Western Australia forms the focal region of the following discussion, which has relevance also for granite exposures in other regions of Australia. People have used the outcrops ever since they first arrived on the continent, primarily as a water source. Aborigines used the rocks as campsites and took advantage of the natural water holes, which were carefully maintained and frequently safeguarded from disturbance by animals and pollution. In contrast, the first Europeans who included nomadic pastoralists quickly modified such water sources by constructing simple wells and dams for use by both humans and stock (Main 1993). Associated with later agricultural settlement and the development of railway networks, large storage dams and tanks were constructed at the base of rocks or across natural configurations of rock topographies (see Laing & Hauck 1997, for review). At the same time exfoliated rock slabs were cemented into walls across the surface of rocks (Plate 1), thereby diverting rainwater from the natural catchment surface and drainage directions. Inevitably, such modifications have had an impact on the biology and diversity of invertebrates, sometimes favourably *e.g.* by increasing habitat resources for some aquatic organisms such as dragonfly larvae, water mites and small crustaceans. However, the overall impacts have been deleterious, particularly for terrestrial invertebrates.

This paper discusses the range of habitats (presented as a template) provided by granite outcrops, that are occupied by invertebrates. It gives an inventory of predominant taxonomic groups so availed, indicates the principal hazards introduced by European usage and how they affect the invertebrate fauna, and promotes a management ideal of salvage and restoration.

Topography and provision of a habitat template

The general image of a granite outcrop is either as an exposed rock pavement or more usually a single dome (monadnock or inselberg (Jutson 1934; Prider 1957, 1985); tor (Main 1967)), or as a complex of such exposures. The outcrops, emerging out of an otherwise subdued or gradually elevated landscape, may be low and platform-like or high with precipitous slopes including "waves" or flared edges. While Twidale *et al.* (1999) suggest that "tor" is perhaps inappropriately used in Western Australia due to it being "increasingly" recognised as "a regional British term", it is arguable to retain the term as understood here in application to either domical outcropping structures or to large boulders, because of its long use in Western Australia from the time of coastal exploration by Vancouver in 1791-2 (Vancouver 1801).

Whether domes (bornhardts of Campbell 1997 and Twidale & Bourne 1998) or platforms, the exposures are variously eroded to form many surface features. Campbell (1997, Table 1) categorised many landforms of granite according to their weathering, constructional and tectonic forms. Main (1997) gave a simplified classification of rocks pertaining to their biological associations as domes, pavements, sub-surface *i.e.* "fugitive" outcrops and boulder piles or "tumuli" (nubbins" of Campbell 1997 and Twidale & Bourne 1998). In this context, the term "tumulus" for a rocky mound was meant figuratively and in no way intended to indicate human construction or rearrangement (*e.g.* a rock lined sepulchral mound or barrow) as interpreted by Twidale *et al.* (1999). Nevertheless because of the possibility of a literal interpretation of my usage, and whether a "nubbin" or not, "rock pile" or "boulder pile" or "rocky hillock" may be more appropriate.

The following examples include most of the erosional features that provide habitats for invertebrates (see also Bayly 1997, 1999; Hussey 1998; Main 1967, 1997). The

HABITATS OF INVERTEBRATES

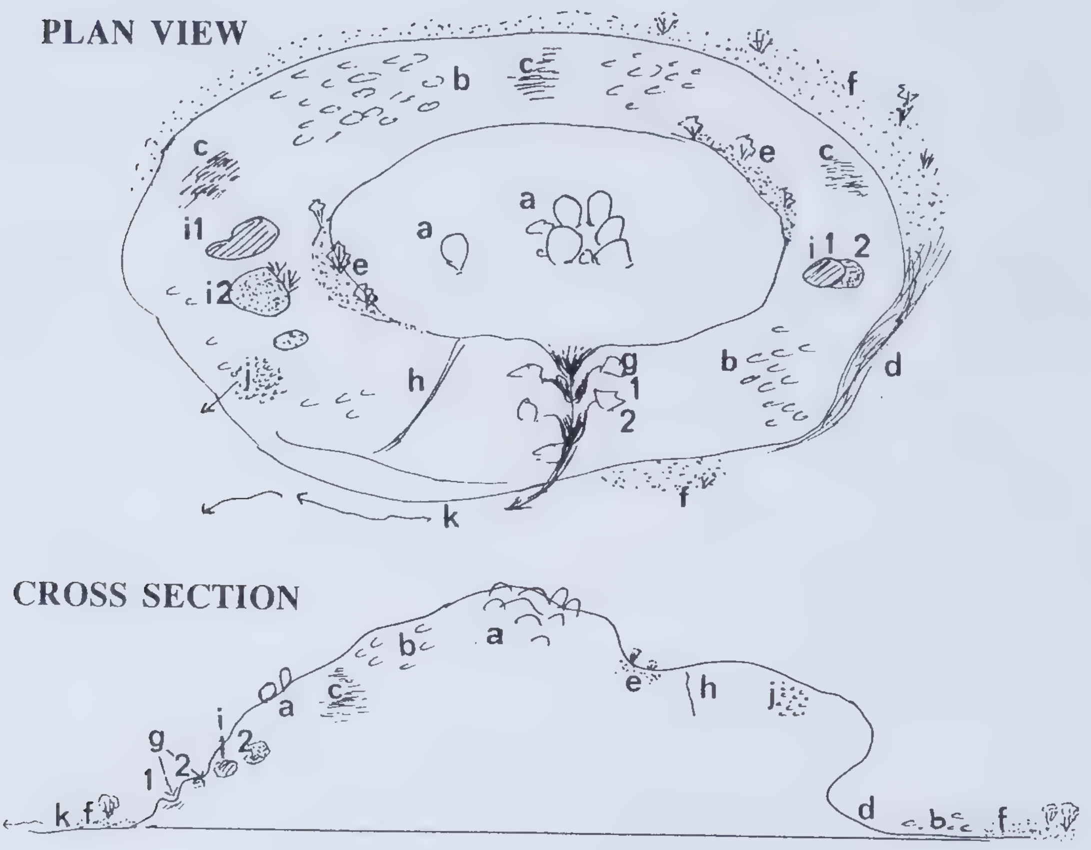


Figure 1. Habitats for invertebrates provided by a granite outcrop. See Table 1 for records of fauna observed in, recorded or collected from respective microhabitats. **Terrestrial:** **a**, rock piles, pedestals; **b**, rock flakes and slabs (partially exfoliated slabs); **c**, lichen, moss swards; **d**, flares or "waves"; **e**, shelves with shrubs and meadow; **f**, apron or peripheral meadow; **g**, tiers of depressions, **g 2**, "Babylonian gardens"; **h**, crevices; **i**, **2** seral meadows. **Aquatic:** **g**, tiers of depressions, **g 1**, "water falls" and stepped pools or gnammas; **i 1**, rock pools or gnammas; **j**, runoff seeps from moss and soil (and "streams"); **k**, peripheral streams (at edge of rock), creeks.

topographic position of these respective habitats on granite outcrop configurations is indicated in Fig 1.

Terrestrial habitats

(a) Pedestals, rock piles and tafoni; boulder shadows. Single boulders with narrow bases (pedestal rocks) are frequently sited on the slopes of domical rocks. Rock piles may be sited on the tops or slopes of outcrops or sometimes on hillocks and often comprise loose groups of boulders partly buried in soil. Tafoni are hollowed-out boulders resembling small, partly open caves. These habitats provide shelter for invertebrates amongst the soil and debris at the base of the rocks; shadow areas also are amenable to invertebrate occupation.

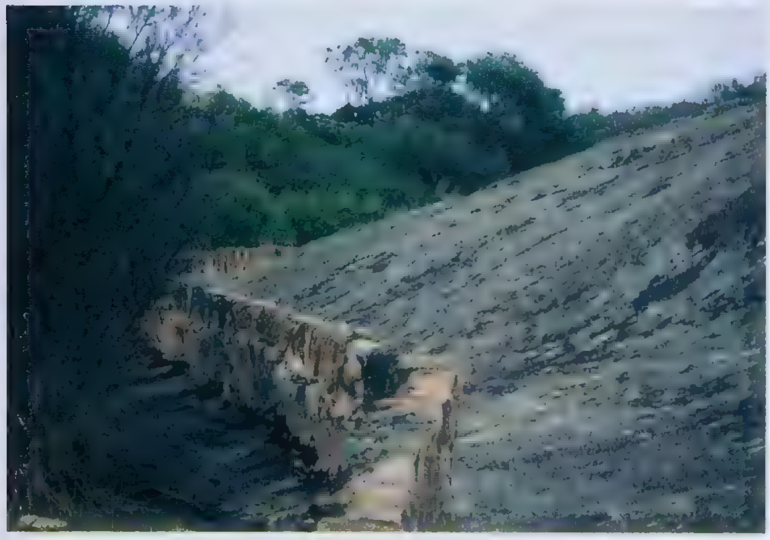
(b) Rock flakes and slabs. These are formed by exfoliation from the parent rock and form permanent or temporary living spaces between the parent rock surface and roof of the flakes. Undisturbed outcrops are generally littered with numerous slabs (Plate 2) but on many outcrops they have been collected and cemented into walls to divert water from the natural catchment slopes (Plate 1) thereby causing habitat deprivation. Small sheets of partly exfoliated rock are an earlier developmental stage to free slabs or flakes; large, partly attached sheets form "A-Tents" (Campbell 1997) and harbour invertebrates.

(c) Lichen and moss swards. These grow wherever a rock surface has weathered and soil has formed. Such mats may be small (a few centimetres) or extensive. If favourably sited, they may hold considerable moisture and also form the head of seepages and associated ephemeral surface streams.

(d) Flares (or waves). These are flat or sloping extensions of the rock surface forming an "edge" which abuts on the apron of soil. Undisturbed outcrops usually have a scatter of exfoliated slabs on the base of the "wave".

(e) Shelves. They are present on most of the domical or higher rocks and even some of the platform types. Depending on the depth of soil deposition, vegetation varies from meadow-type ephemerals, ferns, *Borya*, and rushes to shrubs.

(f) Apron with peripheral meadow. At the edge of the rock, an apron of shallow soil is usually present. Because of the underlying rock floor, these meadows become waterlogged after rain and hence are seasonal (summer-dry) bogs. "Resurrection" plants (Gaff 1981), particularly species of *Borya* that through water loss in summer turn



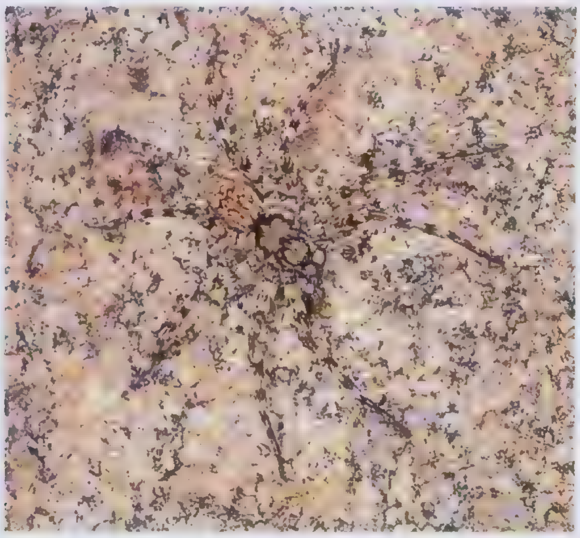


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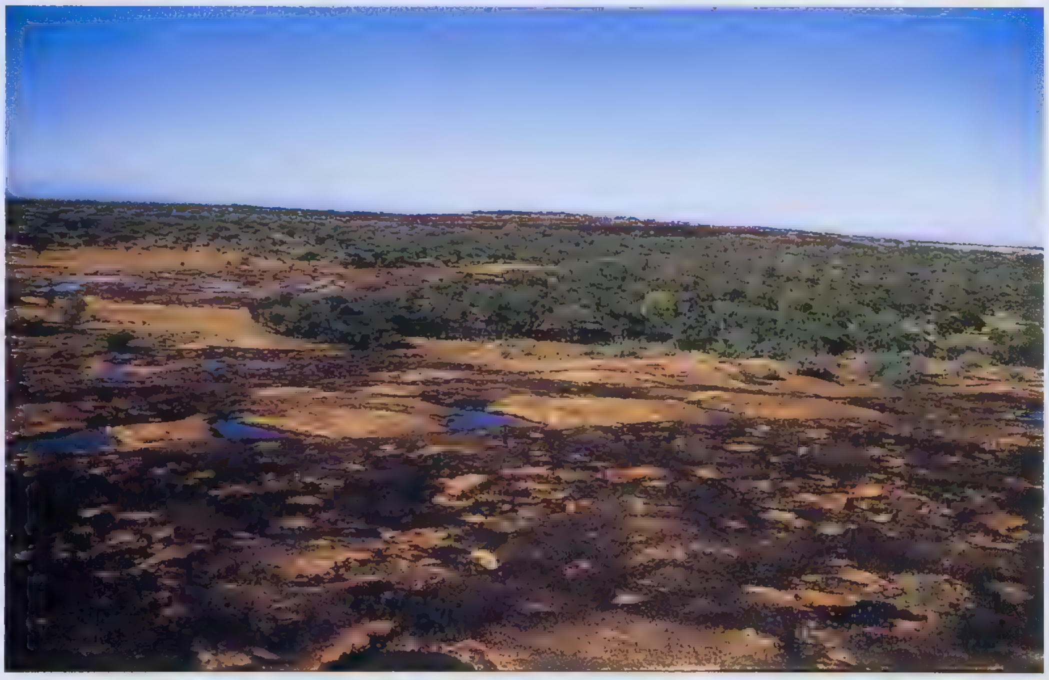
Plate 1. Exfoliated rock slabs cemented into a wall across the surface of a rock, thereby diverting rainwater from the natural catchment surface and drainage directions into a reservoir (Merredin Rock).

Plate 2. Undisturbed outcrops are generally littered with numerous slabs (exposure near Payne's Find).

Plate 3. Seral meadows are usually small, ranging upwards from about 40 cm to several square metres. They are formed by infilling of rock pools (gnammas) on slopes or flat expanses of outcrops (Sanford Rock).

Plate 4. The rock "carpet" wolf spider, so named because of the carpet-like, mottled pattern (photograph by D Elford).



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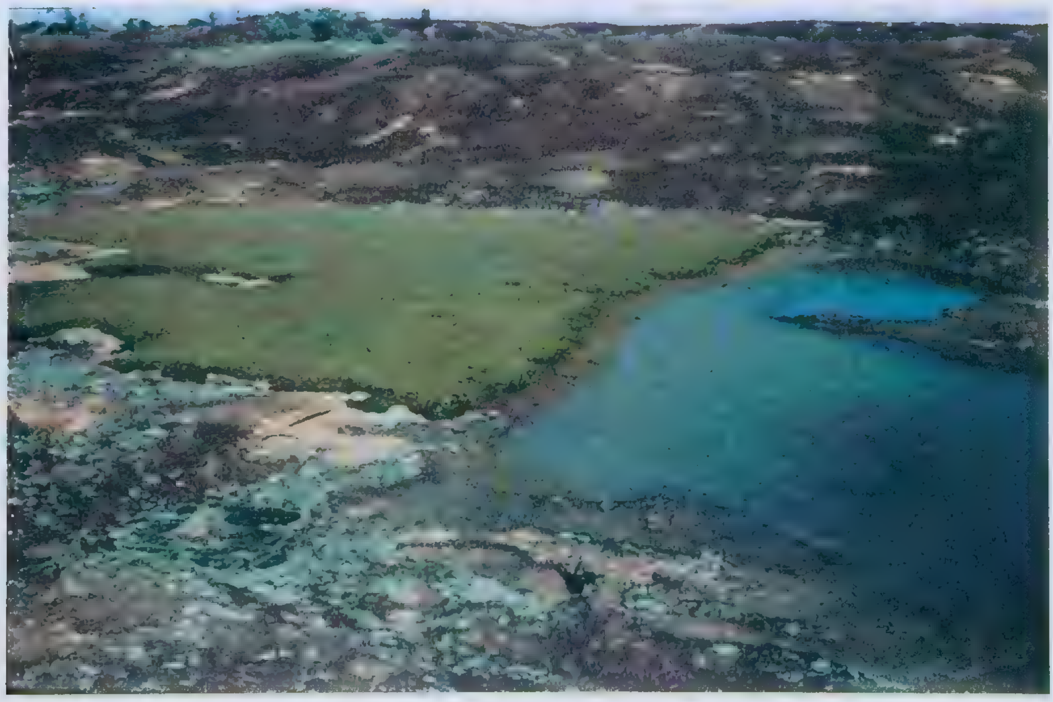

3

orange then green when they rehydrate after rain, are the dominant plants of aprons.

(h) Crevices. These, and vertical cracks, on outcrops frequently shelter mobile invertebrates and occasionally provide a permanent home for sedentary organisms, particularly if soil and debris accumulates. The roots of some shrubs such as *Kunzea*, *Beaufortia* and *Anthocercus* may also penetrate cracks of the rock deep below the perceptible crevice and thus provide further habitat amongst root mats, on bark and foliage.

(i 2) Seral meadows. These meadows are usually small, ranging upwards from about 40 cm to several square metres. They are formed by infilling of rock pools (gnammas) on slopes or flat expanses of outcrops (Plate 3). Depending on their depth they may be vegetated by lichen, moss, ferns, orchids, ephemerals and *Borya*, but occasionally with rushes and small shrubs including *Baeckea*, *Beaufortia* and *Kunzea*.

(g 2) "Babylonian gardens. "Hanging" clumps of vegetation develop in soil that accumulates in tiered gnammas or stepped, pocket-like depressions on the slopes of rocks (see Main 1997, Plate 4). They are thus a late seral stage of the "water fall" sequence of rock pools (g 1).

A specialised and extensive habitat, not discussed here, comprises the algae and thin lichen sheets which mantle the entire surface of granite outcrops. This habitat supports microorganisms that have not been subject to study in the region.

Aquatic habitats

(g 1) Tiers or steps of depressions (gnammas), seasonal rock pools. During and after heavy rain, these develop into cascades or waterfalls.

(i 1) Gnammas or rock pools. These form in depressions of the rock surface and may be shallow (Plate 3) or deep, ranging from a few centimetres in depth to at least a metre. Bayly (1997) and Campbell (1997) discuss the structure and nomenclature of various types of rock holes and pools.

(j) Runoff seeps and streams. Seeps from moss beds, which trickle continuously through the wet season, provide a specialised habitat. Some configurations on rocks also direct runnels of water into localised streams in declivities.

(k) Peripheral creeks. These form around the edges of outcrops and often drain into surrounding bush and woodland. Even when these creeks cease to flow they frequently hold water for long periods in water holes that are able to augment populations of invertebrates beyond the time of the ephemeral rock pools (gnammas).

Habitat occurrences and biology of fauna

There have been few targeted studies of terrestrial invertebrate occurrences on granite outcrops, either as surveys of particular rocks or distribution of particular taxa and their association with a range of rocks. Much of the available information is unrecorded *i.e.* unpublished, or is associated only with taxonomic descriptions. Perhaps the only survey-type study is that of Doronila & Fox (1997), who surveyed the ants of Sandford Rock Nature Reserve. However, in this study only three of the eleven habitat sites surveyed could strictly be regarded as rock or fringing rock habitats. Nevertheless, a substantial number of records have been gleaned from various sources and these are compiled in Table 1.

The aquatic fauna has been subjected to more focused study (Bayly 1982). Bayly (1997) reported on a survey of gnammas on 17 granite outcrops. The biology of a few selected taxa has also been studied either at individual rocks or over their geographic range *e.g.* of chironomid midges including *Archaeochlus* (Jones 1974; Cranston *et al.* 1987; Edward 1989). Again, information obtained from various records is summarised in Table 1.

The precariousness of the overall rock habitat and naturally seasonal drought means that survival of organisms is closely linked to (a) the refugial nature of microhabitats and (b) coincidence of dormant life history stages and unfavourable seasonal conditions. Habitats such as moss swards and those associated with soil and litter accumulation, as on shelves and meadows, are able to absorb moisture from fog as well as rain. Rock surfaces act as catchments even during light rain and mist (Fernie 1930; Laing & Hauck 1997) and some of such water is chanelled into depressions and also captured by moss and lichens. Temperatures on the rock surface can range from over 50 °C (Marchant 1973; Bradshaw & Main 1968) to below zero. Although experiencing extremes of temperature under the flakes, the high temperatures are lower than on the exposed rock surface. Several spider taxa reside permanently under rock flakes; most are web weavers but some are hunting spiders that forage at night thereby avoiding heat stress (as do also their arthropod prey).

A few terrestrial animals are able to burrow *e.g.* mygalomorphs and some lycosid spiders, some scorpions, myriapods particularly millipedes, and insects such as cockroaches. The mygalomorph genus *Teyl* occurs in the meadows of many granite rocks. These spiders aestivate in sealed burrows for months; dispersion of brood young, wandering of males and mating and foraging of spiders takes place during the winter.

Endemicity (*i.e.* restriction to particular rocks) of invertebrates does not appear to be as marked as for plants. Notable known exceptions are in the mygalomorph genus *Teyl* (however the numerous species remain unnamed; Main 1997), the pseudoscorpion *Synsphyronus elegans* Beier which is known only from Yorkrakine Rock (Harvey 1987) and the water mite *Chudalupia meridionalis* from Mt Chudalup (Wallwork 1981). The genus *Teyl* has almost certainly speciated due to isolation around the refugial rocks during onset of arid conditions from late Oligocene through the Pliocene (Main 1999). In contrast many species are widely distributed, even some which are known to occur only on granite rocks. Hence the question arises as to how they are dispersed. While some web-weaving spiders such as the redback (which of course also occurs in other habitats), other theridiids and pholcids disperse on gossamer as spiderlings, the dispersion behaviour of most of the hunting spiders (*Delena* and *Eodelena*, *Rebilus* and *Hemicloea*) is unknown. For spiders and other invertebrate species which are known to occur also in habitats other than granite rocks, such as under bark of trees in surrounding bushland, their occurrence on the rock "islands" is easily explained.

A spider of particular interest is the rock "carpet" wolf spider, so named because of the carpet-like, mottled pattern (Plate 4). This large, unnamed lycosid attributed to *Pardosa* by Main (1976) may rightly belong taxonomically elsewhere. Believed to comprise a single species, it has been recorded from many widely separated rocks. It lives permanently under exfoliated slabs, hunts on the rock at night and appears to be territorial regarding both home "slab" and foraging terrain. Clearly there is much observational and biological work to be done to unravel some of the biological enigmas associated with evolutionary history and dispersion of invertebrates on rock outcrops.

Aquatic organisms comprise two categories. One group shows definite life history adaptations to summer drought and produce dormant eggs, as do many of the crustacean groups or the organisms are dormant as larvae or pupae (*e.g.* certan dipterans) and thus remain *in situ* in the dried out pools on the rocks, revitalising after rain. The other group have no dormant phase. Some have aquatic larvae and either a terrestrial adult phase (some insects *e.g.* dragonflies) or an adult stage, which is amphibious (certain beetles). Alternatively, water mites for example are dependent on an aquatic habitat throughout life and are transported by other organisms (insects or birds) from one water body to another. Such organisms are clearly not confined to rock pools but, like some of the terrestrial organisms enjoy a multi-habitat life style.

Natural hazards and human impacts

Natural hazards are related to weather and climate, including extremes of temperature, occasional floods and wind storms when organisms can be plucked from their habitats and blown away. However flood and wind can conversely also help to disperse some organisms as Main (1997) noted in reference to aeolian reinforcement of fauna on rocks. Over a long time period the fauna can readjust to natural inimical conditions. In contrast the shorter time scale and abruptness of human impacts does not always allow the fauna to restabilise.

Adverse human impacts include;

(a) direct destruction of habitats and foraging on invertebrates, principally the following:

- removal of rock flakes and slabs or translocation of such rock flakes into retaining walls or simply by overturning the flakes in situ thereby exposing the under-surface and damaging the under-rock niche;
- blocking of natural drainage lines on the rock or peripheral creeks and construction of dams (drowning of rock surface areas and environs of peripheral creeks and depleting water source for natural habitats);
- vehicle damage to moss swards, and algae and lichen crusted rock surfaces;
- damage to rock faces (and lichen/algae crusts) by graffiti;
- haphazard dumping of rubbish in sensitive areas;
- pollution of rock pools by washing of superphosphate bags (and construction of small dams on peripheral creeks for the same purpose);
- damage to habitats by feral animals *e.g.* pigs which overturn rock flakes and uproot vegetation while foraging (personal observations); pollution of water bodies by dogs, foxes, donkeys, camels and horses; burrowing and foraging by rabbits;
- destruction of habitats by hooves and decline of vegetation by grazing animals (sheep and cattle) particularly on private property; and
- foraging on invertebrates by foxes;

and (b) indirect and incremental, additional long term effects such as;

- establishment of weeds through dispersal by feral animals including rabbits (see above), farm animals on private property, and dumping of farm animal carcases;
- depletion of or damage to vegetation through browsing and foraging (feral animals and farm stock);
- damage to the soil/debris interface of microhabitats *e.g.* the fragile floor of rock pools, meadows and the apron by feral animals and farm stock;
- physical damage to rock surfaces (see above, particularly the unstudied algae/lichen sheets) by casual hikers; and
- modification of "aesthetic sites" (usualy flat areas on outer edge of apron meadows) by picnickers for provision of vehicle parking, barbecues, rubbish disposal and toilet facilities. On a larger scale, camping and caravan areas jeopardise similar sites.

Conservation and restoration

It is outside the scope of this paper to itemise management and restoration procedures which have been addressed by AR Main (1997), Hussey (1998) and Anon (1999). However, any management and reconstruction procedures need to take into account that the richest habitats for macroinvertebrates are also the most vulnerable. Rock flakes and slabs and rock pools support a diverse assortment of taxa, while the numbers of species known from various rocks are probably only a small proportion of those present over the array of rocks in southern Western Australia. In settled areas, both in the wheatbelt and pastoral areas, many rocks have lost most of their loose flakes to water catchments and vandalism. Throughout the forest and coastal areas, vandalism is also prevalent.

It is not readily apparent to the non-biologist that seemingly barren rocks actually support an array of living invertebrate animals as well as plants. Even the more obvious seasonal life in the rock pools is frequently disregarded. Again, the rock pools are subject to pollution and vandalism. The invertebrate fauna of the moss and lichen swards is poorly known, but likely to be rich in small crustaceans (*e.g.* amphipods), insect larvae and collembolans, tardigrades and earthworms as well as those organisms noted in Table 1.

While translocation of certain vertebrates to restore populations that have been lost is practical, it is probably

Table 1

A preliminary inventory of invertebrate fauna collected or recorded from, or observed in association with granite outcrops. See Fig 1 for explanation of symbols (a - k) representing particular microhabitats. WAM, database of Western Australian Museum, specimen labels indicating association with granite rocks. BYM (Barbara York Main), unpublished observations, field notebook records or specimens in personal collection. MSH (Mark S Harvey), pers comm (observations).

	HABITAT	AUTHORITY
TERRESTRIAL		
ARACHNIDA		
ARANEAE (SPIDERS)		
MYGALOMORPHAE		
BARYCHELIDAE	(b, e, f)	BYM (Withers & Edward 1997)
IDIOPIDAE		
Aganippe spp	(e, k-banks)	BYM (Withers & Edward 1997)
Gaius sp	(f)	BYM (Withers & Edward 1997)
NEMESIIDAE		
Chenistonia tepperi Hogg	(e, f)	BYM; WAM (Withers & Edward 1997)
Teyl spp	(e, f, i 2)	(Main, 1976,1997; Withers & Edward 1997)
Merredinia damsonoides Main	(f)	BYM (Withers & Edward 1997)
Kwonkan eboracum Main	(f)	(Main 1983; Withers & Edward 1997)
Aname diversicolor Hogg	(f)	BYM (Withers & Edward 1997)
ARANEOMORPHAE		
DESIDAE		
Badumna spp	(b)	BYM
Forsterina spp	(b) ?	WAM
DYSDERIDAE		
Ariadna spp	(e, f, i 2)	BYM (Withers & Edward 1997)
GNAPHOSIDAE		
Hemicloea spp	(b)	BYM
LINYPHIIDAE		
Erigone spp	?	WAM
others		WAM
LYCOSIDAE (wolf spiders)		
Lycosa spp	(a, b, c, e, f, i 2)	BYM
Lycosa leuckartii	(b, e)	BYM
"lycosid" as *Pardosa* sp	(b)	(Main 1976; Withers & Edward 1997)
MITURGIDAE		
Miturga spp	(b, e)	(Main 1976; Withers & Edward 1997)
MIMETIDAE		
Australomimetus sp	(b)	WAM
NICODAMIDAE		
Nicodamus mainae Harvey	(b, e, f, i 2)	(Harvey 1995; Main 1976)
OONOPIDAE		
Opopaea sp	?	WAM
PHOLCIDAE (daddy longlegs)	(a, b)	
Trichocyclus spp ?	(a, b)	BYM
PRODIDOMIDAE		
"*Molycria* spp"	(b)	BYM; MSH; WAM
SALTICIDAE		
Adoxotoma chinopogon Simon	?	WAM
SELENOPIDAE		
Selenops spp	(b)	BYM; MSH
SPARASSIDAE =HETEROPODIDAE (huntsman spiders)		
Delena cancerides Walckenaer	(a, b)	(Main 1976)
Eodelena lapidicola Hirst	(b)	(Hirst 1991; Main 1954 as *Delena cancerides*)
STIPHIDIIDAE		
Baiami sp	(b, e)	BYM; WAM
Corasoides spp	(i 2, e, f)	BYM
THERIDIIDAE		
Latrodectus hasselti Thorell	(a, b)	(Main 1976; Withers & Edward 1997)
Steatoda spp	(b)	BYM; MSH
other genera	(b)	BYM; MSH
TROCHANTERIIDAE		
Rebilus spp	(b)	BYM (Bayly 1992; Main1976; Withers & Edward 1997)

Table 1 (continued)

	HABITAT	AUTHORITY
SCORPIONIDA		
SCORPIONIDAE		
Urodacus planimanus Pocock	(b, b/e)	WAM (Koch 1977)
Urodacus sp	(b, b/e)	BYM
BUTHIDAE		
Lychas marmoreus (Koch) ?	(b)	BYM
PSEUDOSCORPIONIDA		
GARYPIDAE		
Synsphyronus elegans Beier	(b)	BYM; WAM (Beier 1954; Harvey 1987; Withers & Edward 1997)
S. callus Hoff	(b)	MSH
S. gigas Beier	(b) ?	(see Harvey 1987)
S. leo Harvey	(b)	(Harvey 1987)
Synsphyronus spp	(b) ?	BYM; MSH
OPILIONIDA (harvestmen)		
CADDIDAE		
Hesperopilio mainae Shear	(e, f)	BYM; WAM (see Shear 1995)
TRIAENONYCHIDAE		
Calliuncus sp	(e)	BYM
Nunciella aspera (Pocock)	(b)	BYM; WAM (Main 1954 ?)
ACARI		
TROMBICULIDAE		
Schoengastia gutekunsti Goff	(b ?)	BYM; WAM
MYRIAPODA		
CHILOPODA (Centipedes)		
Cormocephalus hartmeyeri Kraepelin	(b)	BYM; MSH; WAM
Scolopendra morsitans Linnaeus	(b, f)	BYM
Scolopendra laeta	(b ?)	BYM
GEOPHILIDA	(b, e)	BYM; WAM
DIPLOPODA		
SPHAEROTHERIIDAE		
Cynotelopus notabilis Jeekel	(b, e)	BYM; WAM
PARADOXOSOMATIDAE		
Antichiropus spp	(b, e, f)	BYM; MSH
ONYCOPHORA		
PERIPATOPSIDAE		
Occiperipatoides gilesii (Spencer)	(c, e, f ?)	BYM; WAM
CRUSTACEA		
ISOPODA	(b, e, f, g 2)	BYM
AMPHIPODA	(c, e, g 2, h)	BYM

INSECTA (a selection)

(There are undoubtedly many additional specimen records in the WAM and Australian National Insect Collection, CSIRO, Canberra and records scattered through the taxonomic literature; however difficulty of access and time constraints have not allowed thorough documentation for this preliminary account).

	HABITAT	AUTHORITY
Various orders including:		
BLATTODEA (cockroaches)	(b)	BYM
COLEOPTERA	(b, e)	BYM
TENEBRIONIDAE (Piedish beetles)	(b)	BYM
CARABIDAE	(b)	BYM
DERMAPTERA (ear wigs)	(b, e)	BYM
DIPTERA		
STRATIOMYIDAE	(j/f)	BYM
EMBIOPTERA	(a, b)	BYM; (Ross 1991; Withers & Edward 1997)
HEMIPTERA		
REDUVIIDAE	(b)	BYM, MSH
HYMENOPTERA		
ants	(a, b, c, e, f)	BYM
mud wasps	(a, b, h)	BYM (Main 1967; McMillan & Pieroni undated)
LEPIDOPTERA (moth larvae)	(c)	(Main 1967)
ORTHOPTERA (crickets, grasshoppers)	(b, c)	BYM

Table 1 (continued)

	HABITAT	AUTHORITY
AQUATIC		
Selected higher taxonomic categories (Orders & Families) only are given if listed by Bayly (1997, Table 2) for taxa from rock pools (habitat (i 1) as defined here). See also Bayly 1992; Hussey 1998; Main 1967; McMillan & Pieroni undated; and other authorities listed below.		
ARACHNIDA		
ACARI (water mites)		
ORIBATEI	(i 1)	(Bayly 1997)
AMERONTHIIDAE		
Chudalupia meridionalis Wallwork	(i 1)	(Wallwork 1981)
ARRENURIDAE		
Arrenurus balladoniensis Halik	(i 1)	MSH
CRUSTACEA		
ANOSTRACA (fairy shrimps)	(i 1)	(Bayly 1997; Main 1967; McMillan & Pieroni undated)
CLADOCERA (water fleas)	(i 1)	(Bayly 1997; Hussey 1998; Main 1967; McMillan & Pieroni undated)
CONCHOSTRACA (clam shrimps)	(i 1)	(Bayly 1997; Main 1967; McMillan & Pieroni undated)
COPEPODA (copepods)	(i 1)	(Bayly 1997; Main 1967)
NOTOSTRACA (shield shrimps)	(i 1)	(Bayly 1997; Main 1967)
OSTRACODA (seed shrimps)	(i 1)	(Bayly 1997; Hussey 1998; Main 1967; McMillan & Pieroni undated)
INSECTA (larval and/or adults)		
DIPTERA		
CERATOPOGONIDAE	(i 1)	(Bayly 1997; McMillan & Pieroni undated)
CHIRONOMIDAE	(i 1)	(Bayly 1997; Main 1967; McMillan & Pieroni undated)
Archaeochlus Brundin	(j)	(Cranston, Edward & Colless 1987; Edward 1989)
GERRIDAE	(i 1, k)	(McMillan & Pieroni undated)
COLEOPTERA		
DYTISCIDAE	(i 1)	(Bayly 1997; Main 1967; McMillan & Pieroni undated)
GYRINIDAE	(i 1)	(McMillan & Pieroni undated)
HYDROPHILIDAE	(i 1)	(Bayly 1997; McMillan & Pieroni undated)
HEMIPTERA		
CORIXIDAE	(i 1)	(Bayly 1997; Hussey 1998; Main 1967; McMillan & Pieroni undated)
NOTONECTIDAE	(i 1)	(Bayly 1997; McMillan & Pieroni undated)
ODONATA	(i 1)	(Main 1967; Hussey 1998; McMillan & Pieroni undated)
TRICHOPTERA (caddis flies)	(i 1, k)	(Main 1967)
PLATYHELMINTHES	(i 1)	(Main 1967; Bayly 1997)
NEMATODA	(i 1)	(Bayly 1997)

Note: dominant habitats are the most vulnerable; predominantly rock pools (i 1) & rock flakes (b); run off seeps (j) important for relictuals.

not an option for invertebrates except possibly for some of the larger species (spiders and myriapods). Restoration and protection of habitats would seem to be the immediate pragmatic approach.

Acknowledgments: I greatly appreciated the effort of M S Harvey in searching the Arachnida and Myriapoda databases of the Western Australian Museum for references to granite outcrop occurrences of specimens and for his permission to cite personal observations.

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Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates

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Abstract

Pools and streams on granite outcrops in south-western Australia are reliably filled, but highly seasonal, freshwater habitats that support a diverse array of aquatic invertebrates. A recent biological survey of the wheatbelt has more than doubled the number of invertebrates, to at least 230 species, known from these habitats. Granite outcrops contribute significantly to endemism in the aquatic fauna of the inland south-west and have particular conservation value for about 50 species, mostly rotifers, microcrustaceans, phreodrilid oligochaetes and chironomid midges, restricted to them. Outcrops may also be important for the wider aquatic invertebrate fauna as a freshwater habitat, if salinity in the Western Australian wheatbelt continues to increase.

Keywords: Granite outcrops, aquatic invertebrates, wheatbelt, conservation.

Introduction

Granite rock outcrops are a conspicuous feature of the dscape in south-western Australia. Their weathered d fractured surfaces often hold water in small pools of ferent dimensions, varying from small deep holes to ad flat-bottomed depressions and elongate crevices yly 1999). The pools are filled by rainfall, usually in nter, and persist for several weeks or sometimes for nths, depending on their size, morphology and the e of year they fill. An additional aquatic habitat on nite outcrops is the ephemeral streams draining from ols, and from saturated moss beds, into marshy und around the perimeter of the outcrop or into rrounding streams. These pool and stream habitats are abited by invertebrates that are able to deal with their nporary nature by having strong powers of dispersal sects), adults that do not require water (most insects), drought-resistant stage such as a resting egg (*e.g.* ifers, copepods) or silk-encased larvae (some ronomid midges).

A number of publications have dealt with the ecology systematics of particular aquatic invertebrates urring on granite outcrops in south-western Australia Linder 1941; Edward 1968, 1989; Jones 1971, 1974; ddes 1981; Cranston & Edward 1987, 1999; Frey 1991, 8; Liehne 1991; Smirnov & Bayly 1995; Benzie & Bayly 6; Maly *et al.* 1997). At the community level, Bayly 82, 1997) provided records of aquatic invertebrate emblages from 26 outcrops in the south-west and cussed the strategies used by invertebrates to survive such seasonal environments. More general accounts of nite outcrops, their fauna and conservation are given Bayly (1992, 1999).

In this paper, we present the results of a survey of atic invertebrates from pools on 9 granite outcrops. ese were sampled during a biological survey of Western Australian wheatbelt wetlands carried out as part of the State's Salinity Action Plan (Anon 1996) by the Department of Conservation and Land Management. The wheatbelt is a large area of dryland agriculture in south-western Australia, approximately bounded by the 600 mm average annual rainfall isohyet to the west and the extent of land clearing to the east (Fig 1). In this region a large proportion of wetlands are severely degraded by increasing salinity and other problems associated with rising water tables. The survey was designed to provide information on the distribution of biodiversity in the region to assist conservation planning. The survey results, together with previously published work, are used to compile an updated list of taxa from aquatic habitats on granite outcrops. The biodiversity, distribution and conservation of the aquatic invertebrate fauna of granite outcrop pools are discussed.

Materials and methods

A list of taxa previously recorded from granite outcrops was compiled from publications listed in the Introduction, with minor emendations resulting from taxonomic changes. For this list, records of the occurrence of taxa in individual pools sampled by Bayly (1982, 1997) were amalgamated to provide data on frequency of occurrence on whole outcrops. To this list were added data from 9 granite outcrops (Table 1, Fig 1) sampled during the Salinity Action Plan biological survey (henceforth referred to as the 'SAP survey'). All outcrops were within the wheatbelt, except Wannara Rock, which was located 10 km east of the line of land clearing. Codes for undescribed species in the list are those used in a voucher collection and database maintained by the Department of Conservation and Land Management, Woodvale. At each of the 9 outcrops, 2 samples were collected; 1 benthic sample using a 250 μm-mesh sweep-net and 1 plankton sample using a 50 μm-mesh net. Use of a plankton net with fine mesh allowed the first

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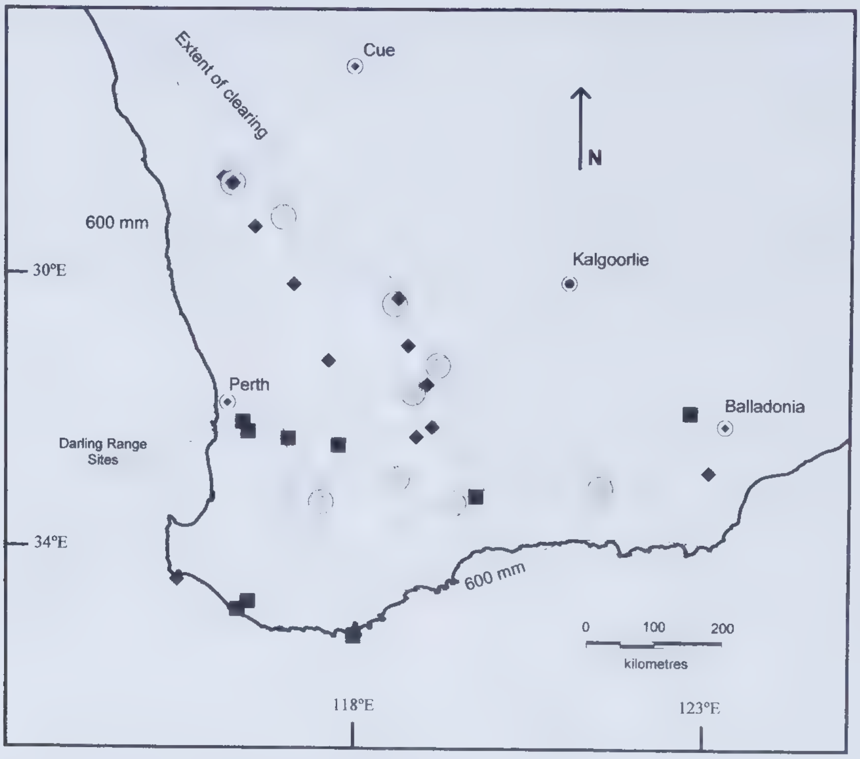

Figure 1. Map of south-western Australia showing granite outcrops sampled by Bayly (1982) (■), Bayly (1997) (◆) and during the SAP survey (◎).

collections of rhizopods and rotifers from the region's granite outcrops. Where possible, sufficient pools (usually >10) were sampled to give a total sweep length of 50 m per sample. Material from separate pools was combined prior to preserving the benthic sample in 70 % alcohol and the plankton sample in 10 % formalin. Samples were sorted in the laboratory. The same methods were used to sample 140 other wetlands (including 40 fresh, <3 g L^{-1} TDS) in the central and southern parts of the wheatbelt during the SAP survey.

Water samples were taken from a single pool at each of the 9 outcrops in the SAP survey for analysis of nutrients (total persulphate nitrogen and phosphorus), chlorophyll (*a,b,c,* phaeophytin), total dissolved solids, turbidity, colour, alkalinity and ionic composition (Eaton *et al.* 1995). pH was measured in the field using a WTW Multiline P4 meter and probe.

The SAP survey outcrops were plotted on ordination axes (semi-strong-hybrid multi-dimensional scaling) on the basis of their invertebrate assemblages, for all taxa identified to species level and for just those species restricted to outcrops. This was performed using the PATN analysis package, presence/absence data with singletons masked and a β-value of –0.1 (Belbin, 1993).

Table 1

Granite outcrops sampled in the wheatbelt of south-western Australia during the Salinity Action Plan wetland survey.

Site	Date	Locality	Description and Tenure
1. Frog Rock	23 Sep 1997	31°29′49″S 119°13′57″E	Large domed outcrop. Jilbadgie Nature Reserve.
2. Cairn Rock	24 Sep 1997	31°51′31″S 118°50′39″E	Large domed outcrop. Cairn Nature Reserve
3. Dingo Rock	6 Aug 1998	33°00′34″S 118°36′08″E	Large domed outcrop. Walled to channel water to dam. Water Reserve within farmland.
4. Dunn Rock	8 Aug 1998	33°20′11″S 119°29′37″E	Large domed outcrop. Dunn Rock Nature Reserve.
5. Puntapin Rock	12 Aug 1998	33°19′31″S 117°24′02″E	Large domed outcrop. Shire Reserve.
6. Styles Rock	7 Sep 1998	33°07′35″S 121°48′02″E	Small flat outcrop, with few shallow pools. Shire Reserve.
7. Yanneymooning Rock	11 Sep 1999	30°40′50″S 118°33′10″E	Large domed outcrop. Yanneymooning Rock Nature Reserve.
8. Wannara Rock	8 Sep 1999	29°31′27″S 116°47′32″E	Large domed outcrop with artificially dammed (50cm deep) pool with macrophytes. Pastoral lease.
9. Pintha Rock (=War Rock)	28 Jul 1999	29°04′22″S 115°59′51″E	Small flat outcrop with few shallow pools. Shire Reserve.

Results

Chemical measurements at 1 pool from each of the 9 SAP outcrops are listed in Table 2. All pools were fresh and contained low concentrations of nutrients and phytoplankton (as indicated by chlorophyll concentration). Most had circum-neutral pH (5.81-7.53), though Styles Rock (site 6) was more alkaline. Sodium and chloride dominated ionic composition, except at Frog Rock (site 1) where calcium concentration was unusually high for a granite pool. This water sample was taken from the largest pool at Frog Rock, which was comparatively deep (about 40 cm) and had deeper than average sandy sediment.

Approximately 230 species of aquatic invertebrates have now been recorded from granite outcrop pools in south-western Australia (Appendix). This is a conservative figure because some groups, such as most bdelloid rotifers, nematodes, turbellarians, some annelids, and a few dipteran and beetle families, have not been resolved to species level. Inconsistencies between studies in degree of taxonomic resolution and in coding of species not formally identified also hindered an accurate estimate of regional richness. However, a plot of cumulative species richness versus number of outcrops sampled during the SAP survey (Fig 2) suggests additional sampling is unlikely to increase richness much beyond 250, unless additional groups are resolved to species level. Of the taxa in the Appendix, 190 were collected during the SAP survey. Previous studies recorded about 115 species, about two-thirds of which were also collected in the SAP survey. The Appendix includes the first records of rhizopod protozoans, rotifers, aquatic oligochaetes and numerous insects from granite outcrop pools in south-western Australia. Groups that lack active dispersal, lack ready passive dispersal, and/or do not have drought-resistant life-stages (such as oligochaetes other than a few granite-restricted phreodrilids and molluscs), are notably less diverse on granite outcrops than in other freshwater wetlands. Few species of water mites were collected even though their larvae parasitise the adults of actively dispersive insects such as beetles and flies.

Previous studies (listed in the Introduction) revealed a number of species restricted to granite outcrops in south-western Australia, including the fairy shrimp (*Branchinella longiristris*), cladocerans (*Plurispina chauliodis, Plurispina multituberculata, Daphnia jollyi, Macrothrix hardingi*), ostracod (*Ilyodromus candonites*), copepod (*Boeckella opaqua*), oribatid mite (*Chudalupia meridonialis*), mosquito (*Aedes occidentalis*), larvae of non-biting midges (*Botryocladius petrophilus, Allotrissocladius* spp, *Archaeochlus brundini*) and several undescribed microcrustacea listed by Bayly (1997). In addition to the above species, D Edward (The University of Western Australia) has recently collected 4 new phreodrilid oligochaetes and 2 more species of *Archaeochlus*, all from the same habitat as *Archaeochlus brundini* (seepages from moss beds at the headwaters of temporary streams), while the SAP survey recorded 34 possibly new species that are currently known only from granite rocks. Some of the latter species, listed in Appendix with a "*cf*" before the species name, are only tentatively separated from the nominate form and some, particularly chydorid cladocerans and ostracods, are likely to be synonymous with undescribed species listed by Bayly (1997). Nonetheless, existing information suggests about 50 granite outcrop species (see Appendix), representing about one-fifth of the total invertebrate fauna of outcrops, are currently known only from this habitat.

Table 2

Water chemistry of pools on 9 granite outcrops in the wheatbelt surveyed as part of the Salinity Action Plan survey of wheatbelt wetlands (see Table 1 for site details). Cation and anion concentrations given as % of total.

	Site								
	1	2	3	4	5	6	7	8	9
pH	7.15	6.73	5.81	7.12	6.77	8.81	6.33	7.53	7.30
TN (μg L^{-1})	400	570	390	640	810	600	630	550	750
TP (μg L^{-1})	10	10	<10	10	10	10	<10	20	40
chlorophyll (μg L^{-1})	0	1	3	1	15	1	3	6	33
Turbidity (NTU)	2.0	1.7	2.0	1.0	7.0	0.5	4.5	2.2	7.0
Colour (TCU)	<5	14	6	23	14	31	2.5	18	16
Total Dissolved Solids (g L^{-1})	0.03	0.11	0.04	0.03	0.03	0.08	0.08	0.09	0.04
Alkalinity as $CaCO_3$ (mg L^{-1})	3	10	3	3	3	8	3	15	10
Hardness as $CaCO_3$ (mg L^{-1})	19	<10	<10	<10	<10	13	13	11	<10
Silica (mg L^{-1})	1	4	<1	<1	<1	1	1	2	1
Sodium (% Meq)	39.04	78.15	78.15	76.76	59.95	70.57	65.85	85.82	71.24
Calcium (% Meq)	44.78	6.90	6.90	7.34	13.75	10.12	10.79	2.66	9.08
Magnesium (% Meq)	12.30	11.37	11.37	12.09	22.67	16.68	17.79	8.77	14.96
Potassium (% Meq)	3.83	3.54	3.54	3.76	3.53	2.59	5.53	2.73	4.65
Manganese (% Meq)	0.05	0.05	0.05	0.05	0.10	0.04	0.04	0.02	0.07
Total cations (Meq L^{-1})	0.669	0.724	0.724	0.680	0.363	0.986	0.925	1.875	0.550
Chloride (% Meq)	60.44	89.48	52.04	69.96	73.10	72.72	65.32	71.47	51.44
Bicarbonate+Carbonate (% Meq)	19.65	8.90	12.69	17.06	15.28	18.65	9.55	18.91	38.15
Nitrate and Nitrite (% Meq)	0.07	0.01	0.05	0.06	0.06	0.03	1.01	0.02	0.05
Sulphate (% Meq)	19.83	1.61	35.22	12.91	11.57	8.59	24.11	9.59	10.36
Total anions (Meq L^{-1})	0.420	2.585	0.650	0.484	0.540	0.969	0.863	1.736	0.603

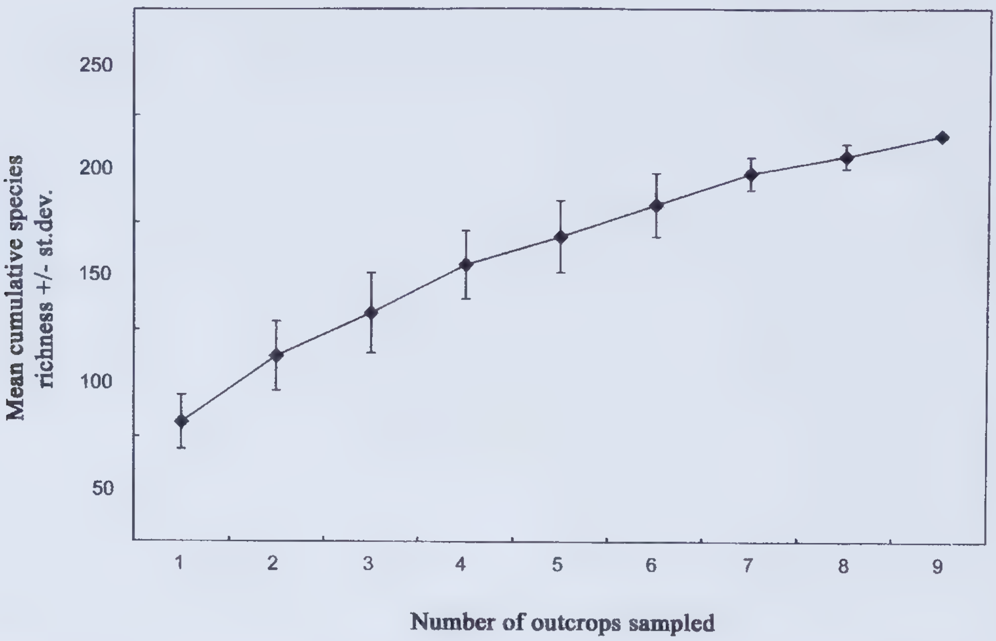

Figure 2. Mean cumulative species richness for the 9 granite outcrops sampled during the SAP survey, calculated from 10 randon re-orderings of outcrop sequence. Values are mean ± standard deviation.

Among the new species collected only from granite outcrops during the SAP survey are rotifers (*Asplanchnopus* and *Trichocerca*), chydorid cladocerans (*Alona*, *Celsinotum* and *Rak*), ostracods (*Limnocythere*, *Cypretta*, *Ilyodromus* and *Cypricercus*), copepods (*Boeckella*, harpacticoids) and oligochaetes (Phreodrilidae). Some chironomids (especially some of the Orthocladiinae) are probably also undescribed (D Edward, University of Western Australia, personal communication). The ostracod genera *Cypericercus* and *Ilyodromus*, in particular, appear to have undergone considerable radiation in granite outcrop pools (Appendix). The record of the rotifer *Taphrocampa selenura* from Pintha Rock (site 9) is the first time this cosmopolitan species has been recorded in Western Australia.

Some species in the Appendix that are not restricted to granite outcrop pools occurred in this habitat at a disproportionately high frequency during the SAP survey. Thus, for 32 species granite outcrops accounted for 50 to 100% of all wheatbelt records, despite outcrops representing only 14% of freshwater sites and 6% of all sites.

The most speciose invertebrate groups at the 9 SAP outcrops were dipterans (especially chironomids) and ostracods, although beetles and clacocerans were also well represented (Table 3). The proportions of different groups varied considerably among outcrops, with insects accounting for between 35 and 60 % of the fauna at any 1 outcrop. Like community composition, species richness varied widely (27-77 species), with some outcrops

Table 3

Species richness of major invertebrate groups for the 9 granite outcrops surveyed as part of the Salinity Action Plan (see Table 1 for sites).

	Site									
Invertebrate group	1	2	3	4	5	6	7	8	9	Mean
Protozoa	0	0	2	0	0	1	1	3	1	0.9
Rotifera	3	0	4	8	0	1	3	12	5	4.0
Cladocera	9	11	3	7	3	0	7	5	2	5.2
Ostracoda	4	5	7	11	8	3	11	12	7	7.6
Copepoda	2	1	2	2	3	1	1	5	0	1.9
Coleoptera	4	8	8	11	5	7	6	12	0	6.8
Diptera	16	12	9	12	6	7	7	10	9	9.8
Hemiptera	2	3	1	6	3	1	1	2	3	2.4
Odonata	6	4	1	1	5	0	0	4	3	2.7
Other Insects	3	3	1	2	0	0	2	3	2	1.8
Other non-insects	3	4	6	5	5	6	7	9	8	5.9
Total	52	51	44	65	38	27	46	77	40	48.9

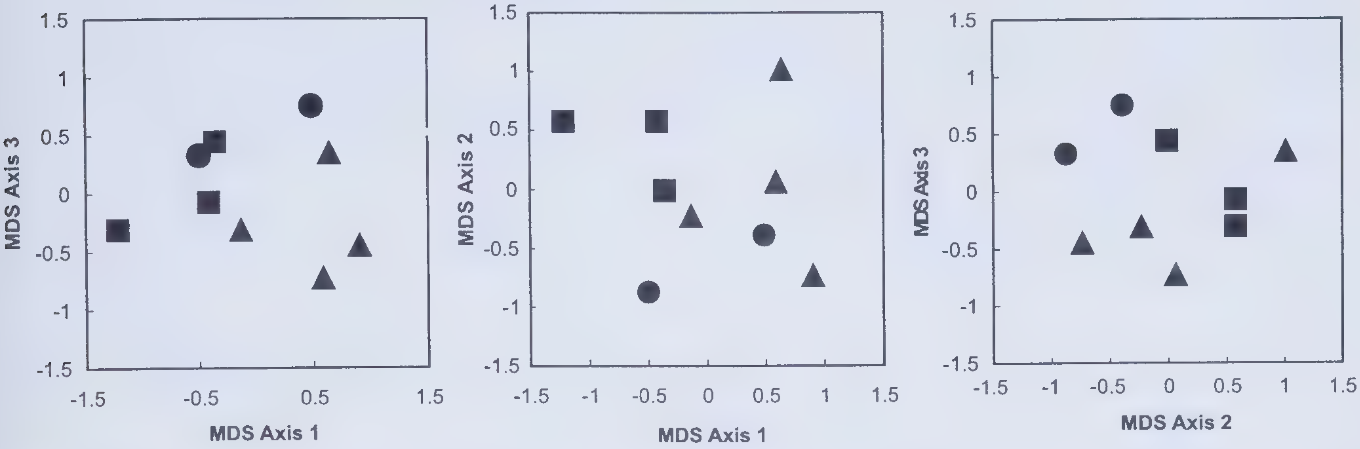

Figure 3. Three-dimensional ordination of the 9 SAP survey granite outcrops based on the component of invertebrate assemblages restricted to granite outcrops, showing relative positions of outcrops in the northern (■), central (●) and southern wheatbelt(▲). Stress = 0.12.

rivalling the more speciose wheatbelt lakes and swamps. The proportion of the overall fauna at the 9 SAP outcrops recorded from any 1 outcrop varied between 13 and 39 %, with a mean of 24.9 ± 7.6 %. Most taxa were rare, with 47 % occurring at only 1 outcrop and 83% at <4 outcrops. The species restricted to granite pools occurred at about the same frequency as the fauna overall, with 43 % occurring at only 1 outcrop and 82 % at <4 outcrops. This pattern of infrequent occurrence applied to insect as well as microinvertebrate groups, with individual beetle species occurring at an average of 2.2 outcrops, dipterans 2.1, rotifers 1.5, cladocerans 2.0 and ostracods 2.5. Even most of the granite outcrop obligates, such as *Daphnia jollyi*, *Macrothrix hardingi* and *Branchinella longirostris*, occurred at fewer than half the outcrops. The most frequently recorded species were *Rak* sp b, several *Ilyodromus*, *Cypretta baylyi* (the only species to occur at all sites), *Boeckella opaqua*, *Allodessus bistrigatus*, *Sternopriscus multimaculatus*, *Allotrissocladius* sp 1, *Hemicordulia tau*, *Dasyhelea* sp, *Anisops thienemanni* and *Triplectides australis*. Most of these are opportunistic inhabitants of granite outcrops.

Ordination of SAP survey outcrops based on invertebrate assemblages showed little evidence of similarity according to geographic proximity when the full assemblage was included. However, an analysis restricted to species that are known only from granite outcrops showed some separation of outcrops by geographical location (Fig 3). In particular, the 4 southern outcrops (sites 3, 4, 5 and 6) separated from the rest in a plot of axis 1 *vs* 3, the 3 central outcrops (sites 1, 2 and 7) separated from the rest in a plot of axis 1 *vs* 2 and the 2 northern outcrops (sites 8 and 9) separated from the rest in a plot of axis 2 *vs* 3.

Discussion

New information from the SAP survey raises the number of species of aquatic invertebrate known to occur on granite outcrops in south-western Australia from about 115 to at least 230. Although Bayly (1982, 1997) sampled some outcrops near the coast in the south-western corner of the State and along the Darling Range (Fig 1), most of his sites and those of the SAP survey were located in the wheatbelt. Not surprisingly, therefore, more than 95% of species in the Appendix are known from the wheatbelt. The following discussion concentrates on the wheatbelt, because this is where most of the outcrops sampled were located and we have information about the fauna in surrounding wetlands of different types. The aquatic invertebrate fauna of wheatbelt outcrops represents about a quarter of the total wheatbelt aquatic invertebrate fauna, estimated to be at least 800 species (based on extrapolation from the 650 species from the two-thirds of the wheatbelt surveyed to date). The majority of the species recorded from granite outcrop pools seem to use this habitat opportunistically and are common in other types of wetlands, both in the wheatbelt and in south-western or southern Australia generally, or even farther north in the Carnarvon Basin (Halse *et al.* 2000). Data from the SAP survey to date, suggest that 32 widespread species, such as the ostracods *Gomphodella* cf *maia* and *Ilyodromus amplicolis*, cladocerans *Planicirclus alticarinatus* and *Rak* sp b and beetles *Paroster* spp, seem to be more likely to occur on granite outcrops than in other types of wetlands in the wheatbelt. Most of these are strictly freshwater species and granite outcrops may be important for their conservation in the wheatbelt, although they may be found to be common elsewhere as more non-granite wetlands are surveyed.

Previous studies noted about 12 described species restricted to granite aquatic habitats and Bayly (1997) listed numerous microcrustacea (particularly ostracods belonging to *Cypricercus*, *Cypretta*, *Limnocythere*, *Bennelongia* and chydorid cladocerans within *Alona* and *Rak*) that appeared to be new and known only from granite pools. With the results of the SAP survey, the number of species known only from granite outcrops is now about 50, assuming most of Bayly's undescribed species are synonymous with undescribed congeneric taxa recorded during the SAP survey. The richness of the granite rock pool fauna in inland south-western Australia reflects the generally high species richness in seasonal water bodies of this region, where there is increasing evidence of high diversity and endemism, particularly within some microinvertebrate groups (Frey 1991, 1998; Halse *et al.* 2000). Moreover, data from the SAP survey to date indicates that species known only from wheatbelt

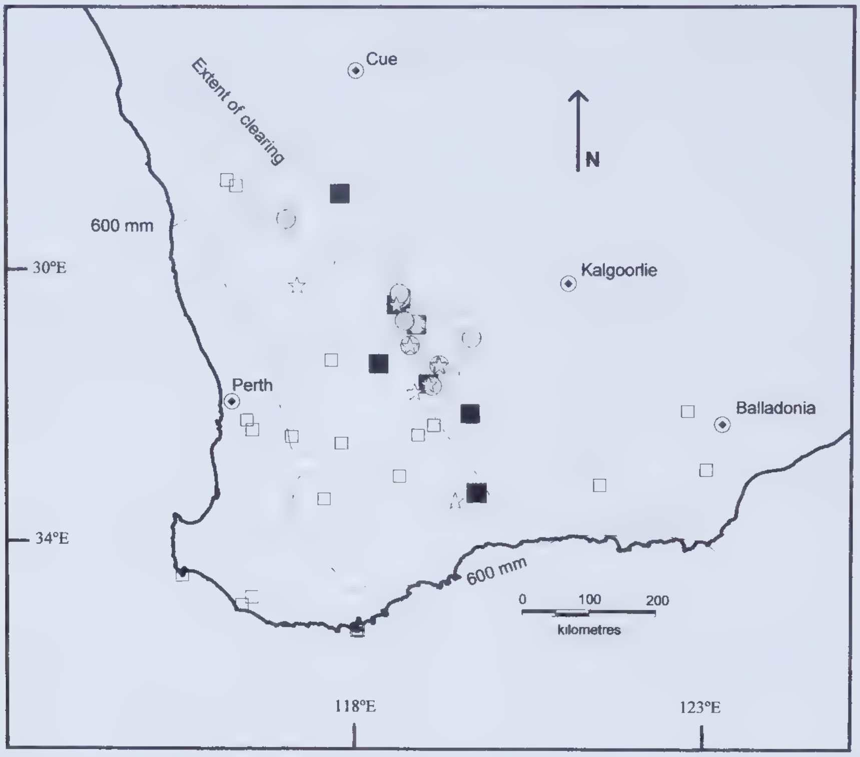

Figure 4. Known records of *Branchinella longirostris* (■), *Macrothrix hardingi* (◍) and *Daphnia jollyi* (☆) on granite outcrops, with outcrops where these species not found (☐) by Bayly (1982, 1997) or during the SAP survey.

granite outcrops are likely to represent at least a quarter of all aquatic invertebrates endemic to the region.

The isolated nature of granite outcrops, and the seasonally stressful environmental conditions experienced there, provide the kind of conditions under which genetic divergence and speciation might be expected (Hopper *et al.* 1997). The number of species apparently restricted to granite outcrops certainly suggests that speciation within some invertebrate groups has occurred in outcrop pools, but more definite comments about likely patterns of speciation are prevented by the absence of finer scale distribution data and an understanding of species relationships within these groups. About a third of species known only from granite outcrops have been collected from only a single locality but whether this reflects recent speciation events without subsequent dispersal or insufficient sampling remains to be determined. The remaining two-thirds are known from more than 1 locality, often 2 or 3 outcrops in the same region of the wheatbelt, although a few (such as *B. longirostris, M. hardingi, B. opaqua, D. jollyi, Limnocythere* sp 636 and *Bennelongia* sp 563) are more widespread, perhaps reflecting varying degrees of dispersal from their origin. The ordination analysis indicates that composition of the obligate granite fauna is more similar between outcrops in close proximity than between more distant outcrops, suggestive of local dispersal from a point of origin.

It seems likely that some species apparently restricted to granite outcrops in the wheatbelt also occur farther inland. Wannara Rock (site 8), which is located 10 km east of the northern wheatbelt, shared a number of new species with outcrops well within the wheatbelt, although 3 others (*Trichocerca* n sp, *Asplanchnopus* n sp and Harpacticoida sp 624) were found only at this site. Many of the species identified as granite outcrop obligates in previous studies are known only from along the eastern edge of the wheatbelt, and may represent the western extent of a more extensive inland range. This pattern is best illustrated by *Branchinella longirostris, Macrothrix hardingi* and *Daphnia jollyi* (Fig 4). *Boeckella opaqua* has a similar distribution but Bayly (1997) also recorded it further east, on Coragina Rock near Balladonia. Bayly (1997) recorded some undescribed species (*e.g. Cypricercus* n sp 2 and n sp 4 and *Limnocythere* n sp?) on outcrops in both the wheatbelt and in the south-western corner of the State, but found a larger number of species apparently restricted to the wheatbelt. Bayly (1982, 1997) found only 4 species (2 ostracods and 2 chydorid cladocerans) were restricted to sites along the south-west coast and none to the 2 Darling Range sites he sampled, although granite outcrops in these areas need to be more extensively surveyed before meaningful comparisons with other regions can be made.

There is general agreement between Bayly (1982, 1997) and the SAP survey data on which taxa tend towards ubiquity at granite outcrops, with *B. opaqua, C. baylyi, I. amplicolis, I. candonites, N.* cf *armata* and *Limnadia* consistently common. In the SAP survey *Rak* sp b, *Ilyodromus* sp 630, *Allotrissocladius* sp 1 and Dasyheleine ceratopogonid midges were also common. There is also agreement on the apparent rarity of most species. For the SAP survey, 47 % of species were collected from single outcrops (of the 9 sampled) while Bayly (1997) found even greater rarity, with 63 % of species present at only 1 or 2 outcrops (of the 17 sampled). There is thus a great deal of heterogeneity in the composition of outcrop assemblages. Similar heterogeneity was recorded for ephemeral pools on the River Murray floodplain, with 43% of 500 species restricted to single sites of the 112 sites sampled by Shiel *et al.* (1998). This heterogeneity is no doubt partly associated with processes of immigration and local extinction, which are usually held to determine the biota of islands (Lomolino 2000). Over longer time scales, speciation may contribute to the uniqueness of the fauna at single outcrops or regional outcrop faunas, but the data suggest this may be only a minor component of overall heterogeneity. Oftentimes, it is difficult to distinguish real differences between sites (caused by the above processes) from apparent heterogeneity in the data caused by limited sampling of sites in time (to account for succession) and space (to account for within site variability).

Succession in the highly seasonal pools of granite outcrops is likely to be a major cause of apparent heterogeneity. Bayly (1982) sampled pools on 2 outcrops on more than one occasion in the same season and noted a tendency for cumulative diversity to increase with time since flooding. Similarly, rapid changes in billabong microinvertebrate community composition after flooding were demonstrated by Tan & Shiel (1993) and Hillman & Shiel (in press). The outcrops sampled during the SAP survey and by Bayly (1997) were each sampled on only one occasion (over periods of 1 to 2 months in winter and spring) and so probably underestimated outcrop richness and exaggerated heterogeneity between outcrops by sampling different outcrops at different times since their pools flooded.

Outcrop pools are more heterogeneous in structure than might be imagined, varying in morphology, chemistry, substrate, presence of rocks providing habitat for insects such as caddis fly larvae, periphyton growth, organic litter and presence of mosses and higher plants. This variation in habitat between pools will also exaggerate heterogeneity between outcrops when few pools are sampled per outcrop. Bayly (1997) mostly sampled 1 or 2 pools per outcrop, but sampled 3 to 4 pools at three of his sites. Of these, Mount Madden pools had 7 to 15 species each but 29 species overall, War Rock had 3 to 14 species per pool and 21 overall, while Petruder Rock had 5 to 14 species per pool and 27 overall, indicating considerable heterogeneity between pools. This suggests that the greater number of pools sampled during the SAP survey (usually 10 per outcrop) would partly account for the higher species richness of 49 ± 15 per outcrop obtained by the SAP survey than the 14 ± 8 by Bayly (1997) and possibly for the lower frequency of species occurrence on outcrops recorded by Bayly (1997).

In summary, granite outcrops in the inland of south-western Australia support a rich and diverse aquatic invertebrate fauna that contributes to high biodiversity and endemism in the wheatbelt. Their fauna consists mostly of opportunistic species that are widespread in the south-west and inhabit a variety of wetland types. For this widespread component, granite outcrops may have an increasingly important conservation role as the wheatbelt becomes more saline over the next few decades (Anon 1996). The primary conservation value of the outcrops, however, is as habitat for the smaller number of species unique to the aquatic habitats the outcrops provide. The apparent heterogeneity between outcrop assemblages, even within this restricted element of the fauna, suggests there may be no such entity as a typical granite pool community. Results to date, showing that very few species occur frequently, with about half found at only a single outcrop, have important implications for conservation planning. They imply that a large proportion of granite outcrops in the wheatbelt will need to be protected to conserve all of the region's granite pool species. More intensive surveys of wheatbelt outcrops, examining seasonal succession at several sites, and of outcrops in the Darling Range and east of the wheatbelt, would show whether this intensity of protection is necessary or whether a subset of more widely distributed outcrops could achieve the same conservation goal.

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Appendix

List of taxa recorded from granite outcrops in south-western Australia. Records from 140 non-granite SAP survey sites are included to show how common species are in the wheatbelt of south-western Australia.

Major group	Family		Taxon	Occurrence in				
				9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
PROTOZOA[†]								
	Arcellidae		*Arcella* sp	3				
	Centropyxidae		*Centropyxis* sp	1				
	Difflugiidae		*Difflugia graman* Penard	1				
		#	*Difflugia* sp a	1				
	Euglyphidae		*Euglyphia* sp a	1				
			Euglyphia sp b	1				
	Nebelidae		*Nebela lageniformis*	1				
MINOR GROUPS								
Flatworms			Unidentified Turbellaria	8				
	Typhloplanidae		*Bothromesostoma personatum*				2	+
Roundworms			Unidentified Nematoda	8			2	+
Tardigrades			Unidentified Tardigrada	2				
ROTIFERA								
	Philodinidae		*Rotaria* sp a	1	5			
			Macrotrachela sp	1	0			
			Unidentified bdelloids	3	0			
	Habrotrochidae		*Otostephanus auriculatus*? (Murray)	1	0			
	Testudinellidae		*Testudinella patina* (Hermann)	1	5			
	Asplanchnidae	#	*Asplanchnopus* sp a	1	0			
	Notommatidae	*	*Cephalodella forficula* (Ehrenberg)	1	0			
		*	*Cephalodella gibba* (Ehrenberg)	1	0			
		*	*Taphrocampa selenura* Gosse	1	0			
	Brachionidae	*	*Brachionus quadridentatus* Hermann	2	1			
			Keratella australis (Berzins)	1	5			
		*	*Keratella procurva* (Thorpe)	1	2			
	Colurellidae		*Lepadella ovalis* (Muller)	2	1			
		#	*Lepadella* cf *patella* (Muller)	3	0			
	Euchlanidae		*Euchlanis dilatata* Ehrenberg	2	5			
	Lecanidae	*	*Lecane flexilis* (Gosse)	2	0			
		*	*Lecane latissima* Yamamoto	2	0			
		*	*Lecane hamata* Stokes	1	0			
		*	*Lecane ludwigi* (Herrick)	5	4			
		*	*Lecane luna* (Muller)	1	1			
		*	*Lecane furcata* Murray	1	0			
	Synchaetidae		*Polyarthra dolichoptera* Idelson	3	1			
	Trichocercidae	#	*Trichocerca* sp a	1	0			
MOLLUSCA								
Snails	Planorbidae	*	*Glyptophysa* sp 3	4	2			
			Isidorella sp	1	9			
ANNELIDA								
Aphanoneurans	Aeolosomatidae		unidentified Aeolosomatidae	1	3			
Aquatic earthworms	Phreodrilidae	#	Astacopsidrilus WA09			3 a		
		#	Antarctodrilus WA21	1	0	3 a		
		#	Phreodrilidae WA10			1 a		
		#	Phreodrilidae WA22			1 a		
		#	Phreodrilidae WA23	1	0			
	Tubificidae		Tubificidae sp	1	59			
ACARINA								
oribatid mites			*Scapheremaeus* sp					1
			Trimaloconothrus sp					1
		#	*Chudalupia meridionalis* Wallwork			b	1	
			Oribatida spp	5	29		2	

Appendix (continued)

Major group	Family		Taxon	Occurrence in				
				9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
Mesostigmatid mites			Unidentified Mesostigmata	3	38			
Trombidioid mites	Trombidiidae		Unidentified Trombidiidae	4	40			
Water mites	Eylaidae		*Eylais* sp	1	17			
CRUSTACEA								
Fairy shrimps	Thamnocephalidae	#	*Branchinella longirostris* Wolf	1	0	3 c, 5 d	1	4
		*	*Branchinella affinis* Linder	1	1			
		#	*Branchinella* cf *compacta*	1	0			
			Branchinella sp					1
Clam shrimps	Cyzicidae		*Cyzicus* sp	2	5			2
	Limnadiidae		*Limnadia* sp	5	0			6
	Lyncaeidae		*Lynceus* sp	2	4			2
Shield shrimps			*Lepidurus apus viridus* Baird			e		
Cladocerans	Chydoridae		*Alona rectangula novaezelandiae* Sars	1	3			
		#	*Alona* cf *affinis* Leydig	2	0			
			Alona rigidicaudis sl Smirnov	2	9		2	3
		*	*Alona macrocopa* (Sars)	4	1		4	
			Alona macrocopa group (4 spp)					1 to 8 each
			Alona intermedia (Sars)				1	
		*	*Alona* sp b	2	1			
			Alona sp n					1
			Alona setuloides? Smirnov & Timms					1
			Allonella excisa (Fischer) group					1
		#	*?Celsinotum* sp a	1	0			
		#	*Celsinotum* cf *hypsilophum* Frey	1	0			
		*	*Dunhevedia crassa* King	1	1			
		*	*Planicirclus alticarinatus* Frey	3	1			2
		#	*Plurispina chauliodis* Frey	2	0		3?	1
		#	*Plurispina multituberculata* Frey				1?	4
		*	*Rak* sp b	6	2			
			Rak sp c (see note f)					5
			Ephemeroporus barroisi sl (Richard)	1	3		3	3
			Monospilus diporus Smirnov & Timms					3
			Leberis aenigmatosa Smirnov			6 g		4d
	Daphniidae		*Ceriodaphnia quadrangula* sl (Mueller)	1	1			
		*	*Ceriodaphnia laticaudata* sl (Mueller)	1	1			
		#	*Ceriodaphnia* sp a	2	0			
			Ceriodaphnia sp				1	5
		#	*Daphnia jollyi* Petkovski	4	0			4
	Macrothricidae		*Macrothrix breviseta* Smirnov & Timms	1	6			2
		#	*Macrothrix hardingi* Petkovski	2	0	8 h		2
			Macrothrix indistincta Smirnov					2
			Macrothrix longiseta Smirnov					1
		#	*Macrothrix* sp a	2	0			
	Ilyocryptidae	#	*Ilyocryptus* cf *smirnovi* Kotov & Timms, 1998	1	0			
	Neothricidae	#	*Neothrix* cf *armata Gurney*	5	0		6	12
	Moinidae	*	*Moina micrura* ? Kurz	2	0			
			Moina sp					3
Ostracods	Limnocytheridae	*	*Gomphodella* cf *maia* DeDekker	1	1			
	Cytheridae		*Limnocythere mowbrayensis* Chapman		3			5
		#	*Limnocythere* sp 636	4	0			
		*	*Limnocythere* sp 557	1	0			
			Limnocythere spp (approx 3 spp)					1 each
	Cyprididae		*Bennelongia barangaroo* sl De Deckker	5	8		1	5
		#	*Bennelongia* sp 563	4	0			
			Bennelongia sp					2
			Candonocypris novaezelandiae (Baird)	1	11			1
			Alboa sp					1
		*	*Cypretta baylyi* McKenzie	9	8		6	11

Appendix (continued)

Major group	Family		Taxon	Occurrence in				
				9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
		#	*Cypretta* cf *globosa*	2	0			
		#	*Cypretta* sp 647	2	0			
		#	*Cypretta* sp 648	2	0			
			Cypretta sp					9
			Kapcypridopsis asymmetra De Deckker				1	
		*	*Ilyodromus amplicolis* De Deckker	6	0		3	8
		#	*Ilyodromus candonites* De Dekker	7	0		4	3
		*	*Ilyodromus dikrus* De Deckker	1	0			
		*	*Ilyodromus* sp 566	3	0			
		#	*Ilyodromus* sp 573	1	0			
		#	*Ilyodromus* sp 630	7	0			
			Ilyodromus sp					6
			Heterocypris incongruens (Ramdohr)					1
		*	*Cypericercus unicornis* De Deckker	1	0			
			Cypericercus salinus De Deckker	2	1			
			Cypericercus sp 442	1	2			
		#	*Cypericercus* sp 634	2	0			
		#	*Cypericercus* sp 637	1	0			
		#	*Cypericercus* sp 643	2	0			
		#	*Cypericercus* sp 638	1	0			
			Cypericercus spp (approx 7 spp)					1 to 6
	Cypridopsidae		*Sarscypridopsis aculeata* (Costa)	1	30			2
		#	*Sarscypridopsis* sp 631	2	0			
		#	*Sarscypridopsis* sp 642 (nr aculeata)	1	0			
Copepods	Centropagidae	#	*Boeckella opaqua* Fairbridge	6	0		1	9
			Boeckella triarticulata (Thomson)	1	68			3
			Calamoecia ampulla (Searle)		15			1
	Cyclopoidae		*Microcyclops varicans* (Sars)	1	3			2
			Metacyclops arnaudi (Sars)		15		1	
			Metacyclops sp					2
			Mesocyclops australiensis (Sars)		8			1
		*	*Australocyclops similis* Morton	2	2			
			Mixocyclops sp				1	
	Harpacticoida	#	Harpacticoida sp 624	1	0			
		*	Harpacticoida sp 674	2	1			
			Harpacticoida sp				1	1
INSECTS								
Beetles	Dytiscidae		*Allodessus bistrigatus* (Clark)	8	36			3
			Liodessus inornatus (Sharp)	2	12			
			Paroster michaelseni Regimbart	3	0			
			Paroster niger Watts	3	4			1
		*	*Paroster couragei* Watts	1	0			
			Antiporus gilberti (Clark)	3	27			
			Sternopriscus multimaculatus (Clark)	6	26			2
			Necterosoma penicillatus (Clark)	3	49			
			Necterosoma darwini (Babington)	1	4			1
		*	*Necterosoma wollastoni* (Clark)	1	1			
			Megaporus howitti (Clark)	2	19			2
			Lancetes lanceolatus (Clark)	2	20			1
			Eretes australis (Erichson)	1	5			1
			Rhantus suturalis (MacLeay)	1	10		1	
			Platynectes sp (larvae only)	1				
	Hydrophilidae		*Berosus approximans* Fairmaire	2	18			1
			Berosus discolor Blackburn	1	29			
			Berosus macumbensis Blackburn	2	15			
			Berosus nutans (MacLeay)	3	4			
			Enochrus maculiceps (MacLeay)	1	4			
			Limnoxenus zeylandicus (Broun)		12			1
	Scirtidae		Scirtidae	2	13			
	Limnichidae		Limnichidae	1	3			
Fly larvae	Tipulidae		Tipulidae	1	23			

Appendix (continued)

Major group	Family	Taxon	Occurrence in				
			9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
	Culicidae	*Aedes alboannulatus* (Macquart)	2	5	i		
		# *Aedes (Finlaya) occidentalis* (Skuse)	2	0	i		
		Culicini sp	1	9			
	Ceratopogonidae	*Bezzia* sp 1	1	24			
		Bezzia sp 2	1	23			
		Other *Bezzia*	4	12			
		Culicoides sp	4	82			
		Monohelea sp 1	1	0			
		Atrichopogon sp a	1	2			
		Ceratopogonidae sp a	1	4			
		Dasyhelea sp	6	13		1	3
	Tabanidae	*Tabanidae*	1	48			
	Dolichopodidae	*Dolichopodidae*	2	49			
	Sciomyzidae	*Sciomyzidae*	1	6			
	Ephydridae	*Ephydridae*	3	64			
	Muscidae	*Muscidae*	1	35			
	Chironomidae	# *Archaeochlus brundini* Cranston *et al*			a		
		# *Archaeochlus* sp a			a		
		# *Archaeochlus* sp b			a		
		Procladius paludicola Skuse	3	73			
		Procladius villosimanus Kieffer	1	29			
		Ablabesmyia notabilis Skuse	3	16			
		Ablebesmyia sp					1
		Paramerina levidensis (Skuse)	1	31			
		# Tanypodinae sp a	1	0			
		* Tanypodinae sp c	1	1			
		Parakiefferiella sp a	2	5			
		* *Compterosmittia* sp a	1	1			
		# *Botryocladius* sp h	1	0			
		# *Gymnometriocnemus* sp f	3	0			
		# *Allotrissocladius* sp m	2	0			
		# *Allotrissocladius* sp l	6	0			
		# *Allotrissocladius* spp			e	1	2
		# *Botryocladius petrophilus* Cranston & Edward	1	0	j		
		Orthocladiinae spp					3
		Tanytarsus bispinosus Freeman	2	16			
		Tanytarsus sp a	2	59			
		* *Tanytarsus* sp b	2	1			
		Chironomus tepperi Skuse	2	35		1	2
		Chironomus cf *alternans* Walker	4	56			
		Dicrotendipes cf "CA1" of Cranston	2	6			
		Dicrotendipes sp					1
		Kiefferulus martini Freeman	1	9			
		Polypedilum nubiferum (Skuse)	3	38			
		Polypedilum cf *watsoni* Freeman	1	4			
		# *Paratendipes* sp a	4	0			?1
		Paraborniella tonnoiri Freeman	3	4	e		?1
		Cryptochironomus griseidorsum Kieffer	1	25			
		Cladopelma curtivalva (Kieffer)	2	36			
Mayflies	Baetidae	*Cloeon* sp	1	2			
True bugs	Veliidae	Veliidae	2	6			
	Corixidae	*Sigara mullaka* Lansbury		4		1	1
		Sigara sp	1	9			
		Agraptocorixa eurynome (Kirklady)	1	11			
		Agraptocorixa parvipunctata (Hale)	5	13			4
		Diaprepocoris personata (Hale)					1
		Micronecta robusta Hale	4	43			4
		Micronecta annae Kirkaldy					2
		Micronecta gracilis Hale	2	17			1
	Notonectidae	*Anisops thienemanni* Lundblad	6	36		1	5
		Anisops hyperion Kirkaldy	2	24		1	3

Appendix (continued)

Major group	Family	Taxon	Occurrence in				
			9 rock SAP sites	140 other SAP sites	Other studies, see below	9 rock sites of Bayly (1982)	17 rock sites of Bayly (1997)
		Anisops stali Kirkaldy		2			2
		Anisops baylii Lansbury		11			2
		Anisops gratus Hale		15			1
		Anisops cf *hackeri*				1	
Moth larvae	Pyralidae	*Pyralidae* sp	3	15			
Dragonfly nymphs	Coenagrionidae	*Ischnura heterosticta heterosticta* (Burmeister)	2	6			
		Xanthagrion erythroneurum Selys	1	22			
	Lestidae	*Austrolestes annulosus* (Selys)	1	40			
		Austrolestes aridus (Tillyard)	1	5			
		Austrolestes analis (Rambur)	1	14			
	Aeshnidae	*Aeshna brevistyla* (Rambur)	1	4			
		Hemianax papuensis (Burmeister)	2	30			
	Libellulidae	*Diplacodes bipunctata* (Brauer)	3	8			
		Diplacodes haematodes (Burmeister)	1	22			
		Orthetrum caledonicum (Brauer)	2	24			
	Hemicorduliidae	*Hemicordulia tau* Selys	7	43			
Caddisfly larvae	Leptoceridae	*Oecetis* sp	2	39			
		Triplectides australis Navas	6	35			

# taxa known only from granite outcrops; * taxa for which granite outcrops represented >50% of SAP survey wheatbelt records; † protozoans not consistently picked for 140 other SAP survey wetlands; a, specimens and information provided by D Edward (The University of Western Australia), b, Wallwork (1981); c, Linder (1941); d, Geddes (1981); e, Jones (1971, 1974) and Edward (1964); f, equals *Rak stagnensis* nomen nudum of Bayly (1997); g, Frey (1998); h, Smirnov & Bayly (1995); i, Liehne (1991); j, Cranston & Edward (1999)

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Conservation of native fauna inhabiting granite outcrops – how do you manage it?

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Abstract

Clearing for agriculture in the south-west of Western Australia has left numerous isolated granite outcrops as important refuges for native flora and fauna. Managing those outcrops requires some appreciation of the basic ecosystem processes that influence habitat quality. The abiotic factors that influence granite outcrop ecosystems include conserving soil and nutrients, minimizing excess nutrient input from external source, limiting surface water movements and the associated problems caused by increasing soil salinity, and fire management. Controlling exotic flora (weeds), fauna (feral animals) and pathogens (mostly fungi) are important biotic factors. Judicious use of herbicides and pesticides is also necessary to achieve management goals. In some situations the native flora and fauna can recovery naturally, but this will be dependent on the size of the granite outcrop and the associated fringing vegetation, the number of individual animals remaining and the potential for recruits to disperse into new habitats. Reintroduction of flora and some of the larger fauna species may be possible. However, by necessity some landowners may need to accept that not all outcrops can support all of the species they would like to see. Small animals and invertebrates that can survive on outcrops will invariably be easier to conserve than larger more charismatic species that can not survive indefinitely.

Keywords: granite outcrops, fauna, conservation

Introduction

The history of clearing of the southwest of Western Australia for agricultural development has been well documented (*e.g.* Saunders & Ingram 1987; Hobbs & Saunders 1993). The amount of remnant native vegetation remaining in varous shires encompassed by the southwest wheatbelt varies from 3-31% (Coates 1987). Amongst these small remnants of vegetation are areas of outcropping granite surrounded by narrow belts of woody perennial native vegetation growing on shallow soils (hereafter referred to as granite outcrops).

Until recently little attention had been paid to these granite outcrops or their flora and fauna. Granite outcrops are important areas of plant diversity (Hopper *et al.* 1997) with a high component of endemic species. Far fewer fauna species appear to be restricted to granite outcrops (Withers & Edward 1997; Bayly 1997) but the outcrops seem no less important to fauna as they provide refuges on a seasonal basis and during protracted periods of drought.

With the establishment of funding schemes by both the Commonwealth and State governments to promote biodiversity conservation and regeneration of native habitat within the agricultural landscape, private landowners now have the incentive and the means to integrate native ecosystem management with established farming practices. In those areas where granite outcrops are the main types of remnant habitat left in the landscape there is potential to develop networks of native vegetation with the outcrops as the central hub. If such systems can be established then fauna inhabiting the outcrops can disperse outwards from these refuges, or re-colonize outcrops from which they have become locally extinct.

The theory sounds reasonable, but what are the practical issues that landholders must deal with in order to conserve or re-establish native fauna? To create or maintain a healthy ecosystem that will be able to support a diverse range of species there must be a balance between inputs and outputs. This principle applies to nutrients, water, soil and plant biomass. Many of the activities associated with commercial farming have the capacity to lead, directly or indirectly, to the loss of some basic resources from the ecosystem while introducing excess quantities of others.

Successful management of native fauna is largely about managing the habitat that the animals need to live in. The quality and quantity of habitat that animals need to survive determines both the number of species and the total number of individuals that can inhabit an area. If the basic ecosystem processes that determine habitat quality are missing or incomplete, then small remnants can provide only limited habitat for native fauna. Before examining the potential for granite outcrops to support native fauna it is worthwhile taking the time to understand some of the basic ecosystem processes that determine habitat quality.

Soils and nutrients

The weathering of granite rock to create coarse soils and eventually finer soils is a slow process. Microflora (lichens and mosses) on the rock surface along with rainfall and cycles of high and low ambient temperatures play an integral part in the creation of soils and the release of essential nutrients. These soils and nutrients are washed off the outcrops and accumulate around the base of the exposed granite. Shallow soils can support small plants, usually with shallow root systems. Deeper soils can support a wider array of species including larger, perennial shrubs and trees with deeper root systems. Generally, the more diverse the plant community around the outcrop, the more diverse is the animal community that inhabits the remnant.

Clearing or grazing of the fringing vegetation removes the nutrients faster than they can accumulate. At the same time compaction of the soil by stock and machinery can lead to rapid movement of surface water off the granite outcrop, eroding more soil and nutrients away from the system and into surrounding paddocks. This erosion can be damaging to surrounding crops, but the impact on the granite ecosystem is far greater. The best way to conserve the nutrients and soils associated with granite outcrops is to fence the remnant and exclude domestic stock. Funding schemes such as the Remnant Vegetation Protection Scheme and Natural Heritage Trust's *Bushcare* cater for this type of activity. Integrating the fencing with any future revegetation projects provides for economies of scale and can result in greater ease of management of farm activities.

If the loss of native vegetation and subsequent erosion is due principally to rabbits then it is important to control, and where possible, eradicate them. Agriculture Western Australia staff throughout the State can provide the most up to date advice on how to control rabbits. It is important that landowners obtain such advice as some of the control methods available (*e.g.* pindone grain baits) can pose serious risks to native wildlife if not carried out according to specific instructions.

If stock, feral goats or rabbits are not excluded from granite outcrops then these animals will deposit nutrients into the system in the form of dung. Nutrients can also enter granite outcrops ecosystems in the form of wind-borne dust during spreading of super phosphate. Many native plants, primarily of the Proteacea family (*e.g. Banksia, Hakea, Grevillea*), are not adapted to survive in nutrient-rich environments and can actually be killed by excess quantities of phosphorous and nitrates. The increased nutrients also provide an ideal environment for introduced weed species to establish and out compete the native flora.

Altered fire regimes

Fire is an integral part of native Australian ecosystems, but inappropriate regimes can have significant impacts on small remnants such as granite outcrops. While the exposed granite surface is often unaffected by fire, the fringing vegetation with its linear form is easily damaged. Fires that burn too hot to allow successful regeneration, or too cool to stimulate regeneration from native legume species (*e.g. Acacia* sp), or too frequently to allow any of the plants to reach maturity and begin producing viable seed, can drastically change the quality of granite outcrop habitat. Similarly, fires that burn in late spring may result in germination of seeds that subsequently die during the following hot, dry summer depleting the soil and above ground seed banks.

If exotic weed species have established amongst the fringing vegetation then they can greatly increase the amount of dry fuel that is available during the summer months, increasing the likelihood that a fire will spread, and greatly increase the intensity of the fire. Invasive weeds also have characteristics that enable them to rapidly colonize disturbed sites. Fire can provide enough disturbance to allow weeds to invade or regenerate more quickly than the native flora. It must also be remembered that many of the native plants inhabiting the fringes of granite outcrops live there only because of the moisture available year-round. As such they have very little tolerance of fire and can be removed from the system by fire.

Fire should be intentionally introduced to granite outcrop remnants only after much careful thought. Landowners should have a very clear idea of what they want to achieve with fire, and be sure that the type (*e.g.* hot or cool), size and timing (summer or autumn) of the fire will give the desired result. They also need to consider what impact the fire will have on the survival of those native animals residing on or around the outcrop. In most cases it is the last refuge these animals have in the farming landscape.

Fire is not always a bad thing as it can play an important role in recycling nutrients through the ecosystem. After prolonged fire-free periods most of the available nutrients are locked up in woody plants as above ground stems or below ground root systems. Fires convert woody materials to ash that is then dissolved in rainwater or run-off from the granite outcrop and taken up by regenerating plants. The elevated nature of granite outcrops means that fires that are followed shortly after by heavy downpours can result in the loss of much of the valuable ash and nutrients. In the wheatbelt this is not an uncommon sequence of events during the summer and autumn thunderstorm season, so landowners who consider using fire to manage their granite remnant must be aware of this risk.

Exotic flora

The impact of exotic weed species in terms of their contribution to increased fuel loads has been discussed in the section above. Exotic weeds also compete with native plants for sunlight and water, commodities that can be in short supply in habitats that still possess tall native shrubs or trees. Many of the exotic weeds encountered in our wheatbelt are annual plants, and they do not provide anywhere near as diverse or structurally complex habitats for small animals to live in. Exotic weeds growing around granite outcrops also create problems for farmers as they provide a source of seed that can re-infest surrounding farmland.

The communities of exotic plants that become established in many native remnants are usually dominated by annual grasses. These weeds are predominantly wind-pollinated and provide a little green feed for native herbivores such as kangaroos and wallabies, but offer no rewards to native insects or birds that require pollen, nectar or fruits to survive.

Exotic fauna

Exotic animals such as foxes, cats, feral goats, rabbits (and in the more remote arid areas feral donkeys) can all have significant impacts on the granite outcrops. Exotic herbivores remove native vegetation, prevent regeneration from rootstock or the establishment of seedlings, and introduce nutrients and exotic weed species to the site in their dung. The larger animals such as feral goats and donkeys can physically damage the granite outcrop ecosystem by dislodging small boulders and rock slabs and contributing to erosion by way of the pads or trails they create. They also consume considerable quantities of water from gnammas (rock pools) and damage wet seepage areas at the base of the granite outcrops.

The establishment and spread of exotic weeds is often aided by the grazing of domestic stock or rabbits, providing further reasons to exclude stock and control rabbits. Rabbits provide an attractive food source for foxes and feral cats, and can encourage greater numbers of exotic predators to persist in the area. This ultimately leads to the decline of native fauna as foxes and cats have catholic diets. Controlling rabbits, particularly if 1080 poison baits are used, can lead to a rapid reduction in fox numbers and can also lower feral cat numbers at times. Unfortunately, the benefits are seldom long lasting as dispersing juvenile foxes and feral cats soon move into the vacant habitat. Control of rabbits must be considered as an ongoing part of farm management.

At present control of feral cats is difficult since they are wary of traps, are difficult to shoot, and will seldom take conventional baits designed for foxes. While there is no doubt that feral cats eat a wide variety of native vertebrates and invertebrates (Martin *et al.* 1996), there is little direct evidence to suggest that they are a major threat to wildlife in most parts of the wheatbelt of Western Australia. In contrast the impact of feral cats on native fauna in more arid areas is much greater. Any humane methods that can be used to reduce feral cat numbers should be considered, but it may be more cost effective in terms of labour and materials to direct efforts towards habitat improvement to offset any impacts feral cats might cause.

Reducing fox numbers is an easier task. Breeding vixens and young cubs can be controlled in dens using fumigants, while independent animals can be shot, trapped or offered poison baits (1080 is the only registered bait). Contact your local Agriculture Western Australia office for the information sheets on which techniques best suit your circumstances and how to combine the various techniques with other farm activities. It is important to note that if landowners are using 1080 baits to control rabbits or foxes that farm dogs will be at risk unless they are kept confined while baits are in the field and are adequately muzzled when working in paddocks adjacent to baited areas. Some landowners have already decided that keeping working dogs on their farms in the presence of fox baits is not feasible, while others have learnt this lesson through experience.

Pathogens

There are a few fungal pathogens that can kill native flora and reduce the quality of the fringing vegetation in granite ecosystems. Many people will be familiar with 'dieback' (*Phytophthora cinnamomi*) which affects some eucalyptus species and a large number of Proteaceae species. There are also fungal stem cankers that can severely affect native vegetation.

Recently a new chytrid fungal pathogen (*Batrachochytrium dendrobatis*) has been recorded in Australia, and has been found to kill a number of our native frog species here in Western Australia. Frogs infected with this fungus have already been recovered from the wheatbelt.

None of these fungal pathogens can currently be controlled using chemicals, which means that the most effective means of limiting their effect is to prevent their introduction into an area in the first place. Landowners must take care to avoid transporting soil, plant material or mud adhering to farm vehicles into areas with remnant vegetation. Farm refuse sites should be located away from remnants and down-slope from them so that pathogens are not transported into the remnants by surface run-off.

Salinity

Rising water tables and the dissolved salts that they bring with them to the surface are major threats to remnant vegetation throughout the wheatbelt. Many granite outcrops are located high in the landscape and will not immediately be affected by salinity, but those situated in mid-slope areas or those situated in predominantly flat landscapes will be very susceptible to the effects of salinity. The salt will reduce the quality and quantity of the fringing vegetation and will also directly affect those species of animal (*e.g.* frogs) that require freshwater in which to reproduce.

The solutions to increasing salinity in the landscape have been the subjects of many workshops in their own right and will not be mentioned further here. Suffice to say that conserving natural ecosystems contained in isolated granite outcrops along with their flora and fauna will be difficult if salt problems in the surrounding landscape or drainage catchment are not adequately managed.

Herbicides and pesticides

Modern chemicals used to control plant and animal pests can adversely affect the quality of granite outcrop communities. If the chemicals are used in a manner other than that specified on the labels, then the fringing vegetation can be damaged or killed and the invertebrate and frog fauna can also be adversely affected. Herbicides and pesticides can get into the granite system either from direct application, as spray drift, or by leaching from empty stock drums dumped in or near the outcrop. Care needs to be taken to ensure that farm chemicals do not come in contact with granite ecosystems, unless landowners specifically want to apply them to achieve control of exotic plants and animals. Remember to read the labels carefully, and if in doubt apply them to a very small area initially until the effects are fully known.

Not all herbicides are bad news for granite outcrops. A number of commercial products (*e.g.* Roundup Biactive® and Lontrel®, and grass-selective herbicides such as Fusilade®, Assure®, and Targa®) have been specifically developed for the control of exotic weed species, and have little or no adverse impact on native plant species. All herbicides and pesticides should be used according to the directions on the labels. Remember a little of a good thing is fine, but twice as much isn't twice as good.

The habitat's fine- what about the animals?

Habitat size

Assuming all of the issues mentioned above are in good order or under control, what things limit the range of animal species that a granite outcrop can support? The most important issue is the size of the fringing vegetation relative to the size of the granite outcrop. The larger the outcrop, the more complex it is structurally (*i.e.* boulder piles, crevices) and the wider the fringing vegetation surrounding the granite the more species (flora and fauna) the ecosystem will support and the larger the populations of individual species.

The world of invertebrates is often measured in terms of metres, while those of reptiles and frogs in tens of metres. Mammals and birds on the other hand have home ranges measured in terms of hectares, and some of the carnivorous mammals like chuditch (*Dasyurus geoffroii*) have home ranges of 1000-2000 ha. Clearly, if a granite outcrop is only a few hectares in area it will not be able to support a thriving population of chuditch. However, there is nothing to prevent the granite outcrop from being part of a chuditch home range if the remainder of the landscape caters for its needs.

The larger native mammal species, such as black-flanked rock-wallabies (*Petrogale lateralis*), quenda (*Isoodon obesulus fusciventer*) and woylie (*Bettongia penicillata ogilbyi*) may well have great appeal and receive most of the media attention. However, they are no more important than the trapdoor spiders living in the moss swards at the base of granites, or the tiny crustaceans that live and breed in the gnammas, or the yellow admiral butterflies (*Vanessa itea*) that congregate on the tops of the outcrops in late winter and spring. As custodians of granite outcrops we need to change our thinking a little and accept that each species is as important as the next.

Minimum viable populations

As the native vegetation is lost from the agricultural landscape the viability of native animal populations in remnants has declined. There are many cases where particular species are still present in a remnant or on a granite outcrop but their numbers have reached such a low level that the likelihood of them surviving for many more years is slim. There may not be enough choice of mates or enough habitat to support any young that are produced, or a mechanism for the young to disperse into new habitat. These are all symptoms of imminent local extinction of the native fauna. Being able to increase the size of fringing vegetation around outcrops by fencing and allowing regeneration, or by creating corridors to link adjacent outcrops, or simply creating corridors to other parts of the landscape, are all necessary if small populations of native animals are to increase. For specific details on how to achieve improved management of granite outcrops see Hussey (1998).

Know your fauna

The best way to make decisions about what remedial action is required for any particular granite outcrop is to find out what native fauna exists there. Surveying the native fauna is not as daunting a task as people might first think. There are simple methods that inexperienced people can use to quickly create a list of the main groups of animals that live on and around granites (see Sanders 1999). It is not necessary to be able to name every species encountered, but recognizing that one species is distinct from another and that it requires a particular type of habitat (*e.g.* gnammas, rock slabs, moss swards, hollow logs, *etc*) is important. Simple fauna surveys help define what actions are needed to conserve or restore a granite outcrop community, but more importantly they provide a useful means of raising the profile of many of the lesser known members of granite communities.

Watch and wait

With appropriate care and management many populations of native fauna inhabiting granite outcrops will recover of their own accord. Many of the invertebrates and some of the smaller vertebrates (e.g. frogs) will show signs of recovery within only a few years as they produce many young at a time and can breed for several months each year. Slower breeding species, including many of the reptiles and medium-sized mammals and birds will take longer to show signs of recovery. The sorry state of affairs we see today took decades to achieve, so we must be prepared to accept the fact that it may take nearly as long to reverse the situation.

The same techniques used to determine which species of fauna are present on granite outcrops can be applied to monitor the recovery of particular species, or the increase in the number of species using particular habitats. Some species of bird do not breed on or around granite outcrops at all, but visit them during the non-breeding period of each year. Seasonal use of the habitat the granite outcrop provides is just that, 'seasonal', and it will be influenced by many factors some of which operate in areas remote from the local area of the south-west wheatbelt. The failure of particular bird species to visit a granite outcrop in any year may have nothing to do with the habitat on the outcrop, but may simply mean the birds have found a better resource somewhere else that year. The true value of granite outcrops is seen in times of drought or when fire has temporarily removed alternative habitats.

Re-introducing fauna

For the past four years CALM has been actively re-introducing native fauna (mammals, some birds and one reptile) into areas from which they had become locally extinct. This program (called Western Shield) has been focused primarily on conservation estate (*e.g.* state forest, Nature Reserves and National Parks), but the basic principles are equally applicable to private property. Before any species is re-introduced to an area a strict protocol (Anon 1995) is followed to determine why the species became locally extinct in the first place and to ensure that management practices are in place to combat the threatening process(es). No animals are re-introduced to an area until all of the problems are adequately addressed. A failure to do so means the animals are unlikely to survive and the effort of re-introducing the animals will have been wasted (not to mention the loss of valuable animals for no gain).

If landowners believe they have remnant habitat, including granite outcrops, that might be suitable for re-introducing native fauna (or flora) they are most welcome to contact CALM to discuss the matter. If they can satisfy the same criteria that CALM must meet (*i.e.*)

- adequate size and quality of habitat;
- security of habitat and control of access by livestock;
- adequate control of exotic weeds/predators; and
- adequate fire management

then much is possible. Conserving our native fauna is a task for all members of the community. Given that much of the remaining remnant vegetation and most of the granite outcrops are located on private property there is excellent potential for private landowners to become involved in this vital task. Granite outcrops provide ideal focal points to practice cutting edge conservation of our unique flora and fauna, integrated with modern farming enterprises.

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The value of granite outcrops for mammal conservation in Western Australia

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Abstract

Granite outcrops in Western Australia contribute significantly to the conservation of several species of mammal. In the arid zone and wheatbelt, granite outcrops are particularly important for *Petrogale* spp and the euro *Macropus robustus*. Other species such as brushtail possums and chuditch also take advantage of the extra shelter provided by granite outcrops. The many granite islands off the south coast support remnant populations of threatened terrestrial and marine mammals. Granite rocks provide mammals with refuge from heat and introduced predators, and they are capable of modifying fire and moisture regimes to the benefit of some species. Many of the larger wheatbelt nature reserves contain granite outcrops and these will be important as mammal reintroduction sites for the Western Shield fauna recovery program. Fox control has been shown to be important for medium-sized mammal conservation on granite outcrops. Rock-wallabies in particular increase in abundance and this offers opportunities for nature based tourism. Appropriate management of granite outcrops, including islands, will contribute significantly towards the enhancement of mammal diversity in Western Australia.

Keywords: granite outcrops, mammals, conservation

Introduction

Granite outcrops are a conspicuous feature of Western Australia, particularly in the south-west of the State (Myers 1997). In the wheatbelt, only two percent of the former vegetation remains uncleared and most of this is now in conservation reserve. Many of these reserves contain granite outcrops as this land was considered unsuitable for agriculture and also because of the value of granite outcrops for water harvesting and catchment (Laing & Hauck 1997). Granite outcrops, particularly the larger, more complex outcrops are also valuable to mammal conservation. In the wheatbelt, most medium-sized mammal species have disappeared (Burbidge & McKenzie 1989) and the remaining smaller species are largely confined to the "islands" of remnant vegetation, many of which contain granite outcrops. Many of the most valuable wheatbelt nature reserves, such as Mt Caroline, Tarin Rock, Dragon Rocks and Boyagin, contain granite outcrops. True granite islands off the south coast of WA also support several terrestrial and marine mammal species.

The value of granite outcrops to mammal conservation lies not only in their special characteristics, but also their relationship to the surrounding remnant bushland. While no mammal species is restricted to granite outcrops, several utilise the refuges created in the rock piles and caves. Granite outcrops are also of value because they can create moist refuges in a dry landscape and can modify fire behaviour that may suit some species. They are also important as re-introduction sites for mammals and offer potential for nature based tourism experiences.

This paper reviews the use of granite outcrops by mammals in Western Australia and discusses management options that will enhance these areas for mammal conservation.

Mammals on mainland granite outcrops

Granite outcrops, particularly those containing caves, large boulders and rock piles, offer valuable refuge sites for several, mostly threatened, mammals in Western Australia. Withers & Edward (1997) concluded that no mammals are restricted to granite rocks, although several are rock specialists. Perhaps the most dependent are the black-footed rock wallaby *Petrogale lateralis lateralis* and Rothschild's rock-wallaby *P. rothschildi* which are found only on rocky habitats, including granite outcrops. In the wheatbelt, *P. lateralis* is now restricted to five granite outcrop remnants (Kinnear *et al.* 1998) after once being "fairly plentiful on low rock hills around Beverley and York" (Shortridge 1909). The black-footed rock-wallaby was described by Gould in 1842 from a specimen taken by John Gilbert in the Toodyay area, where it was reported to be "very abundant in rocky districts in the Swan River" (probably on granite outcrops along the Avon Valley) (Eldridge & Close 1995). It is no longer found in this area, although there is a proposal to re-introduce the species to the Avon Valley (Barry Wilson, Paruna Sanctuary, personal communication). Until the 1980's, rock-wallabies and brushtail possums occurred among the well known granite outcrops, Uluru and Kata Tjuta (Baynes & Baird 1992), and it is likely that many of the other 22 species of ground mammal that once occurred in the Uluru-KataTjuta National Park also used these and other granite outcrops for shelter (Reid 2000). Shortridge (1909) recorded the chuditch *Dasyurus geoffroii*

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sheltering in crevices among rocks in the south-west. The euro *Macropus robustus* is usually also found on wheatbelt reserves that have granite outcrops (*e.g.* Billyacatting Hill Nature Reserve; Chapman *et al.* 1981), on granite outcrops in the Darling Scarp near Perth (Morris & Bromilow 1990), the Pilbara (Ealey 1967) and in the deserts (Burbidge & Fuller 1979). In the goldfields, nests of the stick-nest rat *Leporillus* sp have been found in granite outcrops such as Peak Charles (How *et al.* 1988). How *et al.* (1991) reported seven species, either from or immediately adjacent to granite outcrops in the Pilbara; Rothschild's rock-wallaby *P. rothschildi*, euro *M. robustus*, northern quoll *Dasyurus hallucatus*, Woolley's pseudantechinus *Pseudantechinus woolleyae*, little red kaluta *Dasykaluta rosamodae*, common rock rat *Zyzomys argurus*, and ghost bat *Macroderma gigas*.

Mammals on granite islands

Burbidge (1999) reviewed the importance of islands to the conservation of mammals in Australia. Seven terrestrial and two marine mammals are known from the 200 or so islands along the south coast of Western Australia; most of these are granite outcrops. These islands are of particular value to mammal conservation because they have not been cleared, and the fox and feral cat have not become established on any, although goats, black rats and rabbits occur on some. Several mammals are known from the granite islands of the Recherche Archipelago. The tammar wallaby *Macropus eugenii* occurs on five islands off the Western Australian coast, including North Twin and Middle Islands in the Recherche Archipelago (Smith & Hinds 1995). The Recherche Archipelago also supports two sub-species of the black-footed rock-wallaby. *P. lateralis hacketti* occurs only on Mondrain, Wilson and Coombe Islands, while *P. l. lateralis* occurs on Salisbury Island. The quenda *Isoodon obesulus* occurs on Daw Island and the bush rat *Rattus fuscipes fuscipes* is known from seven islands in the archipelago (Abbott & Burbidge 1995). There is a record of a native rodent from Woody Island (in addition to the bush rat), initially identified as the ash-grey mouse *Pseudomys albocinereus* (Goodsell *et al.* 1976) but possibly the western mouse *Pseudomys occidentalis* . Unfortunately, no specimen was taken and the identification was not confirmed and searches for this species in 1991 failed to find it. It is possible that predation and/or competition with black rats led to the disappearance of this species. The quokka *Setonix brachyurus* is found on another granite outcrop, Bald Island, as well as Rottnest Island and approximately 20 restricted sites on the mainland (Sinclair & Morris 1996; P de Tores, CALM, personal communication). The Australian sea-lion *Neophoca cinerea* and the New Zealand fur-seal *Arctocephalus forsteri* also use granite islands along the south coast to haul out on and to breed (Gales *et al.* 1994; Shaughnessy *et al.* 1994).

Values of granite outcrops as refugia

Burbidge & McKenzie (1989) identified the value of rocky outcrops and rock piles to medium-sized mammals as refuges from fox predation, and Kinnear *et al.* (1988, 1998) has demonstrated the value of fox control around granite rocks to the conservation of *P. lateralis*. Mares (1997) points to the value of granite rocks in modifying micro and macro habitats for plants and animals and their role in providing cooler, moister refugia in times of drought, a characteristic of WA. Morton (1990) identifies the destruction of moist refugia (often around rocky outcrops and waterholes) through overgrazing by rabbits, as one of the major factors in the decline of medium sized mammals in the arid zone. In the wheatbelt, water pools on granite outcrops are used by the ten or so species of bat in the region. The better watered vegetation surrounding granite outcrops in seasonally dry areas often provides refuge for species that are normally distributed in moister areas, such as the bush rat which occurs around granite complexes at Frank Hann National Park, to the east of the wheatbelt.

Because of the patchiness of vegetation and the non-flammability of bare rock, vegetation on granite outcrops is often protected from frequent fires, creating a heterogeneous habitat (Bayly 1999). It is possible that the critically endangered Gilbert's potoroo survives only on Mt Gardner at Two Peoples Bay because no single fire has burnt the entire granite mountain. The vegetation surrounding large granite outcrops may also be protected from frequent fire and this may benefit other species that are not necessarily dependent on granite outcrops for shelter such as the little long-tailed dunnart *Sminthopsis dolichura*, ash-grey mouse, and western mouse (Whisson & Kitchener 1995), as well as larger macropods such as tammar wallaby and brush wallaby *Macropus irma*. With many of the wheatbelt woodlands now cleared, those around granite rocks are important for arboreal species such as brushtail possums and red-tailed phascogale *Phascogale calura*.

Management of granite outcrops to enhance mammal conservation

Granite outcrops and the surrounding bushland offer great opportunities for enhancing mammal conservation in the wheatbelt and provide opportunities for nature based tourism experiences for the public. However some management is required to ensure this occurs.

Fox control and re-introductions

Since European settlement, fourteen species of mammal have become extinct in the wheatbelt and another 12 have declined (Burbidge & McKenzie 1989). Fox predation of the medium sized species has been identified as a major factor in this decline (Kinnear *et al.* 1998, 2000). CALM's Western Shield fauna recovery program aims to recover the mammal fauna of the wheatbelt through a broadscale fox control program and re-introductions (Bailey 1996). Because so many of the wheatbelt reserves contain granite outcrops, these areas will play an important role in this program. Numbats have already been re-introduced to Dragon Rocks Nature Reserve (Tony Friend, CALM, personal communication), and woylies to Boyagin Nature Reserve (Kinnear *et al.* 2000). Rock-wallabies have been reintroduced to a granite rock on private property near Querekin. It is proposed to re-introduce at least 12 species of mammal to the wheatbelt. Fox control around mainland granite outcrops, and the prevention of foxes and feral cats from becoming established on islands, will also assist in the conservation of existing mammal populations. Even smaller granite outcrops could have value as refuge sites for wider ranging species such as chuditch. Re-introductions of several species of medium-sized mammals are proposed for Uluru-Kata Tjuta National Park, including rock wallabies and brushtail possums to the Uluru and Kata Tjuta granites (Gillen *et al*. 2000).

Nature-based tourism

Most mammal translocations to granite rocks and their surrounds, at least in the near future, will focus on threatened species and be undertaken to areas with nature conservation as a priority. However in time there will be opportunities to move mammals to areas where viewing by the public will also be an objective. Once established, populations of some mammals lend themselves for interaction with the public, for example brushtail possums, quenda and rock-wallabies. However once native mammal populations have established, the future management of the vegetation around such granite rocks will need to take their conservation into account. Management issues that would need to be addressed include fox baiting in areas where the public have access, frequency of fire, and clearing of vegetation. The loss of habitat through increasing salinity in the wheatbelt is another problem. Another important issue would be the impact of any reintroduced mammal population on the existing native biota and surrounding farmland. Attracting more tourists to focal points such as granite rocks could detrimentally impact on other values such as rock pool flora and fauna. Also once mammals have increased in abundance, species such as tammar wallaby and quenda will readily venture into crops, and chuditch are well known for their liking of poultry.

Rock wallabies in particular, have good potential as subjects for nature-based tourism. Following fox control they rapidly increase in abundance and are a relatively visible species. They are often seen during daylight hours, particularly in the winter months. At Yardie Creek in Cape Range National Park, tour operators have been taking tourists to view rock wallabies for several years and have participated in sighting surveys. Rock-wallabies are also visible to tourists in the MacDonnell Ranges near Alice Springs. In the wheatbelt, rock-wallabies formerly occurred at Kokerbin Rock, a recreation reserve. There is potential to reintroduce rock-wallabies to this site providing fox control was implemented and recreation controlled to a greater extent. Other wheatbelt granite rocks are presently being surveyed as potential for rock-wallaby reintroductions (Michelle Davies, personal communication).

Several mammal species are associated with granite outcrops and islands in Western Australia and these areas play a significant role in maintaining and increasing mammal diversity, particularly in the wheatbelt. The management of these areas needs to take this into consideration. As mammal recovery programs develop there will also be opportunities for increasing public interaction with native mammals. Providing the habitat is kept relatively intact and not degraded through frequent fires, weed invasion and vandalism, fox control is probably the most important management tool available for mammal conservation, not only around granite outcrops, but throughout Western Australia. Preventing the establishment of foxes and other introduced species onto granite islands is essential to maintaining the value of these to mammal conservation in the State.

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Creation of conservation reserves and managing fire on granite outcrops – a case study of Chiddarcooping Nature Reserve in the Western Australian wheatbelt

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Abstract

This paper uses Chiddarcooping Nature Reserve, NE of Merredin in the eastern wheatbelt, as a case study to exemplify the history of reserve creation for the conservation of granite outcrop biodiversity, and the subsequent management of fire risks on the reserve. Conservation through reserves has been a pivotal management strategy in Western Australia during the period of agricultural expansion since World War 2. Perceptions of the significance of granite outcrops have varied, from vital importance to a threatening fire risk. After inclusion in pastoral leases from the 1870s, Chiddarcooping reserve was first created in 1926 to protect its locally important water supplies. A conservation purpose was added and the reserve doubled in area to 2610 ha in the 1960s in response to submissions from Forests Department Superintendant GE Brockway and Fisheries Department Fauna Protection Officer HB Shugg, who opposed an application for agricultural selection. The reserve was further enlarged to 5262 ha and made Class A in 1978 and 1983 respectively following additional biological research revealing important rare and relictual plant populations. Ongoing research to the present has reinforced the importance of the biodiversity values of the reserve.

The enlargement of Chiddarcooping Nature Reserve to its present size was opposed by local authority officials in the 1970s, who argued it was a fire risk. Recorded fires occurred on the reserve in 1975, 1978, 1987 and 2000. Bare granite rock provides a natural firebreak. Consequently, granite outcrops provide habitat likely to harbour plant and animal species seeking refuge from fire. A study of plant communities recovering from the 1987 wildfire on Chiddarcooping Nature Reserve confirms this view. Of 79 perennial plant species confined to granite there, 77% were obligate seeders, killed by fire and recovering only through seed germination. This is a high proportion of obligate seeder species, and suggests that caution should be used when contemplating use of fire on outcrops. Raking firebreaks and leaving the topsoil in place for vegetation recovery may be better for conservation than bulldozing permanent firebreaks, access considerations aside. Similarly, burning heaps pushed up following firebreak construction has long-term ecological consequences near granite outcrops, as it may sterilize soil seed banks and set back regeneration for many years. Fire should be avoided or used rarely on granite outcrops if nature conservation is a significant issue for land managers. At present we have little recorded history and much to learn about managing fire on granite outcrops.

Keywords: nature reserve, granite outcrops, fire, management

Introduction

The creation of public reserves with nature conservation values has a long history in Western Australia (Ride 1965, 1974, 1975; Hopper *et al.* 1979), arguably dating back to 1830 when Surveyor General JS Roe rejected applications for private ownership of land on the site of the future Kings Park (Burton Jackson 1982). As a management strategy, conservation through reserves has been pivotal, especially following World War 2 when bulldozing increased the rapidity with which extensive areas could be cleared for agriculture or other purposes. Reservation protected native biodiversity from such land uses.

Although the specific importance of Western Australian granite outcrops for biodiversity conservation has only been documented in recent decades (*e.g.* Main 1967; Withers & Hopper 1997 and papers therein), these landforms have been of significance to Aboriginal, colonial and contemporary people for many reasons. This significance is vital for successful conservation according to Holland and Rawles (cited in O'Neill & Holland 2000), who have recently proposed that 'conservation is ... about negotiating the transition from past to future in such a way as to secure the transfer of maximum significance'.

However, what is significant to some is inconsequential or even threatening to others. For example, native vegetation in summer-dry south-western Australia is susceptible to fire. Conservation reserves are a concern to land managers and others in terms of fire risk. Yet conservation reserves are highly valued for their natural attributes by a broad sector of the community, and destroying them because of fire risk would be unacceptable. Resolving such dilemmas in relation to the conservation of granite outcrops is a complex issue dependant on local circumstances, community decision-making and scientific input. At present we have little recorded history and much to learn about managing fire on granite outcrops.

This paper uses a single nature reserve in the eastern wheatbelt as a case study to exemplify the history of reserve creation for the conservation of granite outcrop biodiversity, and the subsequent investigation of plant responses to fire on the reserve. The study reveals issues that may be applicable and relevant to managing granite outcrop reserves elsewhere in south-western Australia and possibly beyond. Hopefully, the paper will stimulate others to question and investigate a subject deserving much more elaboration than is possible now.

Fire on granite outcrops

Granite outcrops provide natural firebreaks. Vegetation on outcrops is usually fragmented rather than continuous, and often low in stature and biomass. Moreover, pockets of vegetation may be bordered by areas of sheet rock or boulders containing no flammable material. Consequently, granite outcrops provide habitat likely to harbour plant and animal species seeking refuge from fire. Conversely, frequently burnt granite outcrops are likely to be invaded by fire-tolerant species, including weeds (*e.g.* Porembski 2000; Pigott 2000). If this is so, a precautionary management approach would be to minimise the use and impact of fire on granite outcrops, even in terrain and surrounding vegetation that is frequently burnt.

Fire is an environmental disturbance most commonly seen in vegetation that is seasonally dry, either tropical, subtropical or temperate. For example, the five regions of the world that have a mediterranean climate of cold wet winters and hot dry summers experience fire as a regular perturbation – California, Chile, South Africa, the Mediterranean and south-western and South Australia. Of these regions, south-western Australia and California's Sierra Nevada in particular have extensive granite outcrop systems, which are also to be found to a more limited extent in mediterranean South Australia and South Africa. It is appropriate, therefore, that a paper on managing fire is included in the present workshop proceedings.

Recent work by John Hunter and colleagues on the New England Tableland of northern New South Wales has shed considerable light on the fire ecology of granite outcrops in eucalypt forest and woodland (Hunter 1995, 1999; Hunter *et al.* 1998). For example, Hunter (1999) observed that a number of species dominated granite outcrop vegetation immediately after wildfires in north-eastern parts of his study area — *Acacia adunca* (Mimosaceae), *A. latisepala, Actinotus gibbonsii* (Apiaceae), *Bulbostylis densa* (Cyperaceae), *Micrantheum hexandrum* (Euphorbiaceae), *Muehlenbeckia costata* (Polygonaceae), *M. rhyticarya, Monotaxis macrophylla* (Euphorbiaceae) and *Pelargonium australe* (Geraniaceae).

Immediately after fire, a number of factors favour fast-growing opportunistic herbaceous species and legumes. Such factors include a nutrient rich ashbed, soil enriched by smoke as a stimulant for germination (Roche *et al.* 1997a,b, 1998), full sunlight at ground level, and the removal or significant inhibition of long-lived woody dominants that normally sequester most light and nutrients in unburnt communities.

Hunter (1999) documented the seed germination characteristics of the herbaceous fast-growing short-lived *Muehlenbeckia costata* and *Monotaxis macrophylla* in the glasshouse, and conducted experimental burns in Bald Rock National Park to examine what stimulates the dramatic post-fire response observed after wildfire. He chose outcrops with no evidence of previous fire, outcrops that had been burnt by wildfire one year previously, and adjacent areas of eucalypt forest. Species present before the experiments were recorded. Then treatments such as clearing all vegetation from around the 2 m x 2 m plots prior to burning, or not so clearing, were undertaken to alter the intensity of the experimental summer fires. Species appearing monthly for a year after the experimental fires were recorded on the burnt plots and adjacent unburnt controls on the long unburnt granite outcrops, on the outcrops burnt by wildfire 12 months previously, and in adjacent forest. Within four months of an October wildfire, individuals of the prostrate herb *Muehlenbeckia costata* had spread 2 m and were flowering. They soon extended up to 5 m, and scrambled up adjacent plants to a height of 4 m. Within two years of germination, most plants had died, the few remaining only with 20 cm long shoots, heavily infested by a rust fungus. *Monotaxis macrophylla* was similarly short-lived and fast-growing. Both species had levels of seed viabilty exceeding 60%, but in the glasshouse germination was poor (6%) for *Muehlenbeckia costata*, and failed to occur for *Monotaxis macrophylla*. In the wild, Hunter (1999) found that granite outcrop vegetation had close to 50% of species killed outright by fire and having to recover solely through seed germination — a group called obligate seeders. The remaining half of species could resprout from underground organs or buds deep within protective bark — resprouters. In contrast, surrounding forest had only 12% of species being obligate seeder species killed by fire. The vast majority (88%) were resprouters.

These differences indicate the importance of granite outcrops as a refuge for fire-sensitive species, a recurrent feature of granite vegetation world-wide. The application of frequent fires to such vegetation may cause the local extinction of fire-sensitive obligate seeders because insufficient time elapses for growth to maturity and establishment of a seed bank. This has been observed on the New England Tableland, where heaths dominated by fire-sensitive outcrop shrubs were reduced by frequent fire to grasslands and sedges dominated by common resprouting species such as *Imperata cylindrica* and *Lomandra longifolia*. Similarly, the conversion of forests and shrublands to grasslands on the granitic islands of Bass Strait through frequent burning is well documented. For example, a tall forest of Tasmanian Blue Gum *Eucalyptus globulus* up to 90 m high once dominated the south-eastern corner of King Island. Soon after settlement in the 1830s, it was converted to open grassland through the use of fire (Chester 1997).

Hunter (1999) made an important observation comparing plant species present before and after three experimental fire treatments on granite outcrops in Bald Rock National Park. He found that responses to the treatments imposed were individualistic and based on the surrounding species pool available at each site (outcrop or forest area) and the initial composition of each plot. These results support the initial floristic composition model, where the initial species composition before a disturbance determines the subsequent composition. This is a surprising result as all sites were within relatively close proximity, being within only a few kilometres of each other and consequently within the same local vegetation community. Clearly, the notion of an orderly succession does not hold in these granite outcrop communities after fire. Life is a lottery, and getting to an outcrop first is as important as any advantage in competitive ability after a fire event.

In south-western Australia the importance of granite outcrops as fire refuges emerged from several studies in the 1980s. Perhaps the most famous case has been the Mount Gardner headland on the peninsula of Two Peoples Bay Nature Reserve, east of Albany, whose *Eucalyptus* and *Agonis* low forest with dense understoreys of shrubs and sedges adjacent to granite provided a last refuge for the critically-endangered Noisy Scrub-bird (*Atrichornis clamosus*; Smith 1985, 1987). A fire frequency of less than 10 years led to a reduction and near extinction of populations of these birds, whereas fire frequencies of the order of every 30 to 50 years were likely to lead to steady population growth. Subsequent fire exclusion has affirmed this hypothesis and led to a spectacular recovery of the species, enabling ongoing translocations to granitic terrain on Mt Manypeaks and elsewhere. The importance of Mt Gardner as a refuge from fire was evident from historical air photography, which showed that the extensive bare granite ridges provided a natural network of firebreaks, which prevented the whole area from being burnt at any one time. This is further borne out by the occurrence of rare plants such as *Banksia verticillata* and the relictual moss *Pleurophascum occidentale* on the granite outcrops of Mt Gardner (Hopper *et al.* 1990; Brown *et al.* 1998). The confinement of many rare plants to granite outcrops throughout the south-west was first documented by Rye & Hopper (1981), and emphasized subsequently by Muir (1985), Hopper *et al.* (1990; 1997) and Brown *et al.* (1998). This trend could be due to fire evasion, but rigorous experiments involving a range of rare species are needed to test such a hypothesis.

Building on an extensive series of studies, Hopkins (1985) argued that recovery of south-western vegetation from fire in the semi-arid wheatbelt and adjacent woodlands takes decades. Kitchener (1976) proposed that the average age of vegetation from some 400 wheatbelt locations was 21 years. Newbey (1985) suggested that no

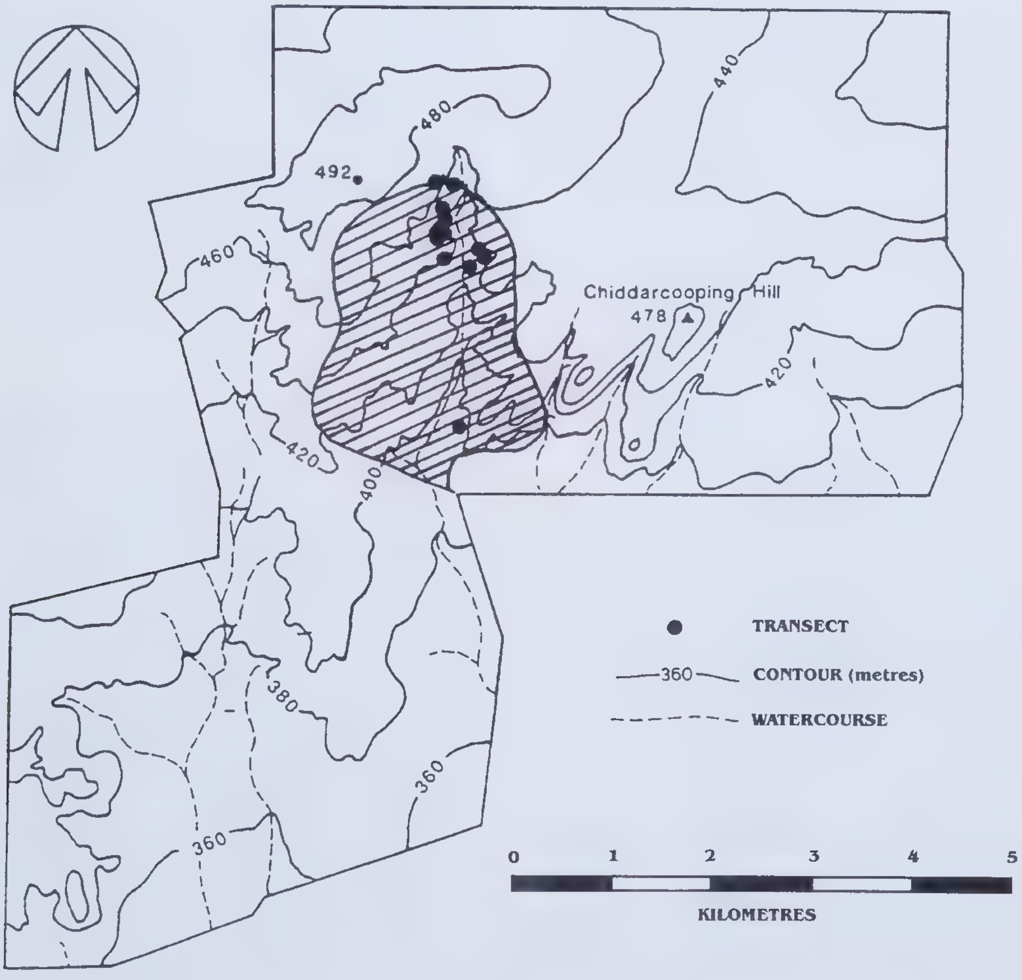


Figure 1. Plan of Chiddarcooping Nature Reserve showing contours, watercourses, transect locations and area consumed by the wildfire of November 1987 (modified from Weston 1985).

evidence of historical fire occurred in granite complex vegetation at the western end of Fitzgerald River National Park, whereas communities such as woodland, dwarf forest, shrub mallee and shrubland all were likely last burnt in the past 40 to 50 years. A wider survey of 300 sites in Fitzgerald River National Park estimated the age of granite outcrop communities including woodlands of *Allocasuarina huegeliana* (Plate 4) and *Acacia lasiocalyx*, as 80 to 100 or more years (Chapman & Newbey 1987).

Weston (1985a) presented historical data suggesting that granite outcrop plant communities on Middle Island in the Recherche Archipelago that were unburnt for possibly 150 years do not lose species, even those opportunists seen only the first year or two after fire, as they are retained in soil seed banks. Storr (1965) found forests 12 to 15 m high of the normally small slow-growing obligate seeders *Callitris preissii* and *Eucalyptus conferruminata* on the granitic Bald Island near Albany, indicating that long periods between fires had preceded his visit. Muir (1985) suggested that the obligate seeder rock sheoak *Allocasuarina huegeliana* (Plate 4) near Quairading may regenerate well in the absence of fire for more than 60 years following the opening of the canopy as old trees die and collapse. Hence, a considerable body of data suggests that granite outcrops might be important refuges for fire-evading species in south-western Australia.

To test the hypothesis that granite outcrops provide refuge for fire-sensitive species, and to develop an understanding of postfire community dynamics in poorly documented mallee and lithic scrub vegetation, I commenced a study on Chiddarcooping Nature Reserve in the Western Australian wheatbelt in 1988. A lightning strike in November 1987 resulted in a significant wildfire that consumed vegetation on granite outcrops in the reserve, and was ultimately contained by a combination of large granite outcrops and a firebreak raked and bulldozed at the time (Fig 1). The bulldozed heaps were subsequently burnt in the spring of 1988 to remove concentrated piles of flammable dead wood and vegetation, as well as to enable future regeneration. This wildfire thus provided an opportunity to examine impacts on and responses of granite outcrop plant communities to fire, as well as regeneration on firebreaks and burnt spoil heaps.

In the present paper, after providing a historical account of the creation of Chiddarcooping Nature Reserve, I summarise early postfire regeneration data from the reserve, and briefly discuss implications for managing fire on granite outcrops. A larger and more detailed analysis of the ongoing post-fire monitoring project will be published elsewhere (C Yates, S Hopper, A Brown & S van Leeuwen, in preparation).

Chiddarcooping Nature Reserve

Chiddarcooping Nature Reserve is located approximately 100 km north-east of Merredin near the eastern margin of the Western Australian wheatbelt (Weston 1985b). It occupies an area of 5262 ha, straddling landforms on the upper slopes of a broad valley trending east-west (Fig 1). There are extensive granite ridges that feed south-flowing ephemeral creeklines within the reserve, as well as lateritic and yellow sandplain uplands overlying granite bedrock towards the northern end of the reserve. The highest point is 492 m, with most of the reserve lying between the 350-450 m contours. The granitoid rock is the most north-easterly occurrence of a medium to coarse-grained seriate granite and adamellite found throughout the south-west on the Yilgarn Block, a craton of ancient Precambrian granitoid rock that has been a continental nucleus for half the age of the earth itself (Chin & Smith 1981).

Annual rainfall is some 300 mm, received mainly in winter, although summer thunderstorms may also deliver significant precipitation. Winters are cool, with occasional frosts, while summer maximum temperatures average 33 °C, with records exceeding 46 °C.

The Kalamaia Aboriginal people

Chiddarcooping Nature Reserve lies within the area occupied by the Kalamaia Aboriginal people, just to the east of the line separating the uncircumcised Nyoongars of the south-west from dry country people who practised circumcision further inland (Maddock 1987). Evidence of Aboriginal occupation is in the reserve. Undoubtedly Chiddarcooping's sources of fresh water and topographic diversity were important, as well as components of its rich biodiversity not found in surrounding woodlands and mallee.

The meaning of Chiddarcooping is not recorded, although 'ing' is widely used in the wheatbelt as a geographical ending, presumably for 'place of' or 'home of', much the same as 'up' is used further south-west (Bindon & Chadwick 1992). The euphonic 'chiddarcoop' is reminiscent of the calls of common nectar-feeding birds such as honeyeaters, which abound at Chiddarcooping (Hopper 1981). The name is also reminiscent of 'chideok', used for 'honeysuckle' (nectar-rich banksias?) by southern wheatbelt Nyoongars, but banksias are not found at Chiddarcooping even though many nectar-rich plants are. The correct meaning of the place name remains a mystery.

European contact and pastoralism

Chiddarcooping Hill was missed by some 20 km by surveyors AC, FT and HC Gregory in August 1846, who traversed country they described as "barren waste" (Maddock 1987) to the north-west and north. Chiddarcooping Hill was included within a pastoral lease first taken up by BD Clarkson in 1874, who set up a hut and sheepyards at Ennuin some 40 km ENE of Chiddarcooping in 1875. A relative of Clarkson, George Lukin, in 1874 drove a mob of sheep from Toodyay to Ennuin in 15 days. In March 1878 Clarkson and Lukin applied to freehold 100 acres around their Ennuin homestead, but their partnership ended by 1880 and Lukin retained the lease, moving his base west from Ennuin to Wilgoyne 20 km NE of the future town of Mukinbudin.

In 1887 Surveyor-General J Forrest introduced new regulations for pastoral leases taken up after that time, applying a 1907 expiry date to ensure the opportunity for more intensive agricultural development. In the winter and spring of 1887, prospectors R Greaves, E Payne and H Anstey, together with an Aboriginal guide from Lukin's Wilgoyne homestead, traversed north-east and

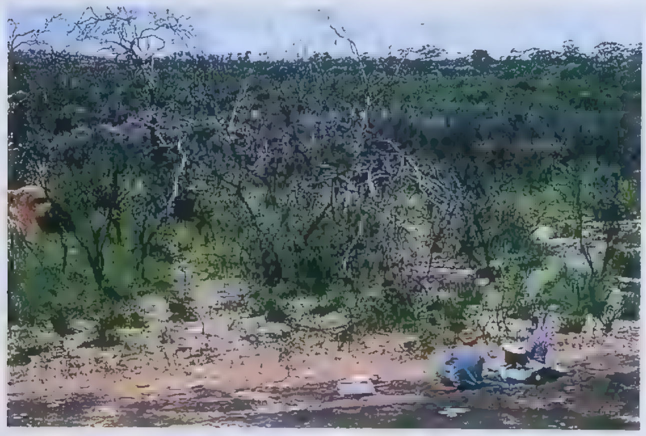


Plate 1. Burnt stand of *Eucalyptus caesia* subsp *magna* resprouting from lignotubers one year after the 1987 wildfire. Other conspicuous resprouters are *Lepdiosperma viscida* and *Xanthorrhoea nana*. Seedlings of *Acacia lasiocalyx* are less than a metre tall. Stephen van Leeuwen and Professor Robert Wyatt in foreground. Chiddarcooping Nature Reserve, November 1988.

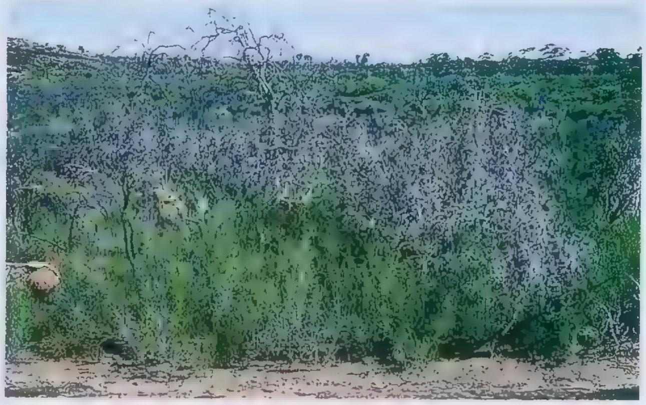


Plate 2. Same stand of *Eucalyptus caesia* subsp *magna* three years after the 1987 wildfire. *Acacia lasiocalyx* forms a dense understorey 2-3m tall beneath the resprouting mallees, which flowered within 18 months of the fire. November 1990.

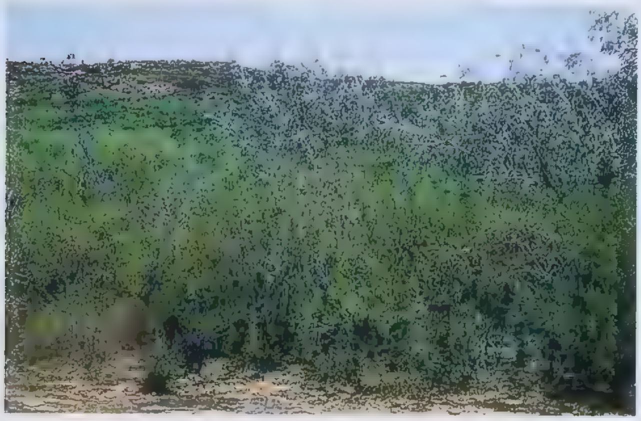


Plate 3. Same stand of *Eucalyptus caesia* subsp. *magna* nine years after the 1987 wildfire. *Acacia lasiocalyx* still forms a dense understorey now 4-5m tall beneath the resprouting mallees. November 1996.

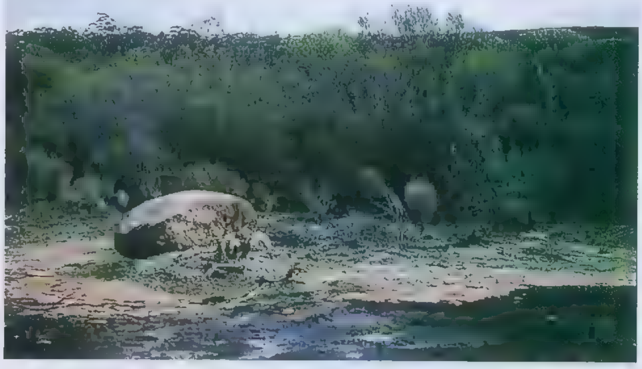
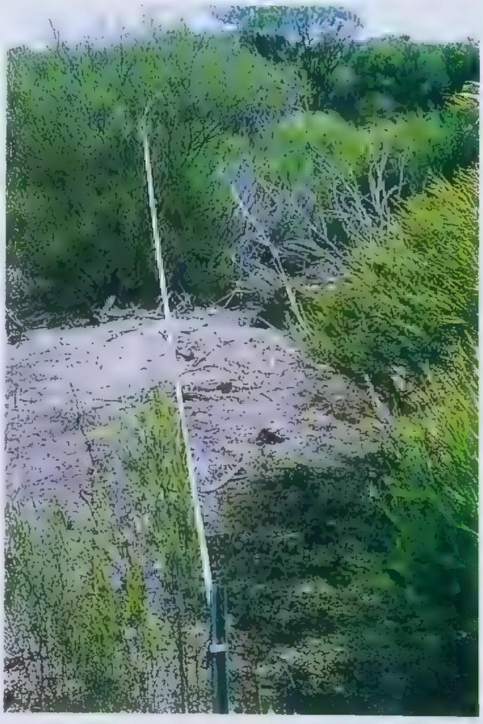


Plate 6. Another site of a bulldozed heap ten years after it was burnt. Note the flaking of surface rock that removed the dark cyanobacterial biofilm and *Grimmia laevigata* moss mats seen in the immediate foreground. Very little recovery of these cryptogams is evident on the spoil heap site. Similarly, the *Borya constricta* herbfield in shallow soil has been sterilized, and shows little sign of recovery. Chiddarcooping Nature Reserve, July 1998

Plate 4. (Left) Two year-old transect 10m x 1m through *Allocasuarina huegeliana* low forest burnt in the 1987 fire. Dr Mark Burgman left and Andrew Brown (obscured). Chiddarcooping Nature Reserve, November 1989.

Plate 5. (Right) Site of transect through bulldozed heap burnt in winter 1988, still with bare sterilized soil nine years after the 1987 wildfire. Normal recovery of the raked firebreak behind is evident. Chiddarcooping Nature Reserve, November 1996.



north from Muckinbudin to Elachbutting Hill and on south-east to Ennuin, where gold was discovered (Maddock 1987). This led to the proclamation of the Yilgarn goldfield in October 1888, with many prospectors passing through the future Mukinbudin area and eastwards to Ennuin thereafter. Because Chiddarcooping Hill lies along this line, it is probable that its plentiful water supplies in winter-spring soon became known and some parties availed themselves of it on the way to the Yilgarn fields.

There are two old stone-lined wells on the nature reserve, indicating water usage by prospectors, sandalwooders and pastoralists in the late 1800s and early 1900s. Moreover, a January 1888 map, prepared by HE Parry after a December 1887 survey, showed three routes to the Yilgarn Hills. One route, suggested by pastoralist Charles Adams of the Mukinbudin district, did indeed run directly east towards Ennuin through Geelakin, just 15 km south-west of and with a clear line of sight to Chiddarcooping Hill. Geelakin was by then leased by George Lukin. The 1888 map had annotated on this route 'This is a road suggested by one of the settlers Mr Adams but there is not any track at present'. Maddock (1987) noted that 'This route through 'Gilakin' later came to be well used enroute to the Golden Valley and Southern Cross'.

In 1888, perhaps after traversing this route, Government Geologist HP Woodward described the country between Mangowine (20 km SW of the future Mukinbudin) and the Yilgarn fields at Ennuin and Golden Valley as 'open', with large alluvial sandy plains in which 'huge masses of intrusive granite stand out in great bold hills' (Maddock 1987).

Official records of Chiddarcooping Hill commenced in a Lands Department lithograph showing areas leased for pastoral purposes at December 31st 1888 (Maddock 1987). The name 'Chiddarcooping' with a 'well' indicated just south-west of it was included on the western boundary of a rectangular lease held by George Lukin. This suggests that Lukin was probably responsible for the two stone-lined wells near Chiddarcooping Hill, and that the Aboriginal name had been adopted by pastoralists in advance of its recording by Government surveyors.

By 1888, Lukin's leases in the Eastern Division totalled 330 000 acres, and he employed a manager Brook Evans to run this vast enterprise. The Chiddarcooping area offered only light grazing around the well-watered granite outcrops, but must have been used often enough to justify construction of the two stone-lined wells. At this time, the Golden Valley mining town south of Ennuin had 314 residents (only 14 were female), two hotels and two stores, providing a significant local market for meat from Lukin's leases.

In 1889, given increasing demand for accurate survey information, 27 year-old mining surveyor HS King was employed on trigonometrical and mining surveys in the Yilgarn. King recorded the aboriginal names for features and localities, as well as details of soil types and vegetation. On March 2nd 1889 he was marking Chiddarcooping Hill as HK54. Geelakin Rock, 15 km to the south-west, was marked subsequently as HK55 (Maddock 1987), so King undoubtedly traversed parts of the present nature reserve. The well within the nature reserve a kilometre or so south-west of the summit of Chiddarcooping Hill was marked as HK64 on another traverse by King. Maddock (1987:12) noted that 'The presence of the high granite rocks must have been a boon to King, for they provided excellent sites from the top of which to take his readings to the next such rock or hill.'

By December 1889, in relation to the eastern wheatbelt, Commissioner for Crown Lands and Surveyor-General JF Forrest wrote that "The greater portion of this division is not likely to be utilised in the near future', due to the lack of rivers. However, Surveyors HS King and C Crossland wrote to Forrest in February 1891 noting that, subject to rainfall, there was a considerable extent of good forest country covered by giant mallee or salmon gum and low scrub, unexcelled in the colony for agriculture (Maddock 1987). Within 20 years Surveyor M Terry was classifying soil types prior to their survey for wheat farms.

By 1893 Lukin was in partnership with George Maddock, running a thriving butchery at Southern Cross. In 1896 Lukin moved to York and Maddock took over his extensive pastoral leases. Sandalwood became an increasingly important local product over the next few decades for Maddock, and the Chiddarcooping area did not escape from rapacious harvest of this aromatic small tree.

In 1901-2 Surveyor Alfred Canning mapped out the No 1 Rabbit Proof Fence in the district from Burracoppin due north (Broomhall 1991). Construction here was subsequently completed by 1904, with the fence passing midway across the 45 km line between Mukinbudin and Chiddarcooping to the east. This saved Chiddarcooping from early attention as a potential farming district. Land near Mukinbudin was made available for agricultural selection in 1910, but the number of settlers was a mere handful until the 1920s. In 1917 the WA Royal Commission on the Agricultural Industry had requested that the Surveyor General FS Brockman draw a line for the northern and eastern limits of wheat growing. His line ran from Burracoppin north-west close to the future townsite of Mukinbudin (Maddock 1987), leaving Chiddarcooping Hill well to the east beyond the intended limit of the wheatbelt.

Chiddarcooping Reserve created

Chiddarcooping reserve was first created in April 1926 for the purpose of "public utility", presumably to protect the wells and water supply for public purposes, but the reserve was not vested for management in any Government authority. At this time it was a quarter of its present size, and included only the south-eastern quadrant of the northern block centred on Chiddarcooping Hill itself (Fig 1). However, Chiddarcooping escaped development as a water catchment. Instead, low stone walls and a large tank for water supply were constructed on Geelakin Rock 15 km to the south-west, which was located closer to the broad valley floor supporting salmon gum and gimlet woodlands favoured by farmers in the district.

Agricultural development was slowed by the Depression and World War 2, but increasing post-war demand led to further land classification surveys, and farms trickled eastwards on suitable land surrounding Chiddarcooping. In 1959, an application from WC, DM and WA Carrod of Mukinbudin to have the reserve released for farming was received by the Under Secretary for Lands, who sought opinions from the Westonia Road Board, the Conservator of Forests and the Under Secretary for Mines in letters dated December 4th (*in litt*, archived files, Department of Land Administration and Department of Conservation and Land Management).

A reply dated December 16th 1959 from the Conservator of Forests, written by Superintendent GE Brockway, noted that Chiddarcooping reserve had negligible forestry value, with only odd patches of wandoo and a few salmon gums, but argued against release for agriculture and for expansion of the size of the reserve to include all the granite outcrop country to the west and north of Chiddarcooping Hill. Brockway put forward four reasons;

1. 'the area is rough and agriculturally unattractive, consisting of some very large massive granite outcrops, large areas of sand much of it with minor granite outcrops, some gravel areas and breakaways,
2. at the time of the (land) classification the rocky areas provided a habitat for some form of rock wallaby,
3. the dense wodgil thickets to the north of the granite rocks provided good protection for mallee fowl, and
4. there are considerable areas of unoccupied land in this locality which appear less unattractive as agricultural propositions but which have not the same suitability for fauna protection.'

Having also received advice from the Under Secretary for Mines who had no objection to Chiddarcooping reserve being made available for selection, on December 23rd the Under Secretary for Lands sought the additional opinion of the Chief Warden of Fauna in the Fisheries Department.

Arguments for a conservation reserve

Superintendent Brockway joined Fauna Protection Officer HB Shugg of the Fisheries Department on an inspection of Chiddarcooping reserve and adjacent land on August 17th 1960. They observed significant flora, with Harry Shugg noting:

'Around the bases of the rocks and in the eroded valleys between them, dense scrub containing acacia, casuarina, melaleuca and calothamnus occurred, while in the areas of deeper soil there were fine specimens of Southern Cross Mallee (*Eucalyptus crucis*) and Gungunnu (*E. caesia*)' (Plates 1, 2, 3). Fauna records included a flock of Major Mitchells, plentiful Singing Honeyeaters, a euro, scats of euro and rabbits, but 'no trace of rock wallabies could be found.'

Superintendent Brockway subsequently wrote to the Chief Warden of Fauna on August 26th advocating the creation of a larger reserve. He noted that

'The rugged inaccessible nature of much of this country, which ensures a large measure of protection to both flora and fauna, coupled with its generally low value for agricultural purposes, makes it well suited for reservation as a flora and fauna reserve... My own view, based on an intimate knowledge gained many years ago as a member of the party which carried out the land classification of this area, plus a recent short refresher examination of it with Mr Shugg, is that the whole area outlined in red should be reserved for the protection of flora and fauna... From the flora angle, I was particularly impressed by several groups of an outstanding strain of Gungunnu (*Eucalyptus caesia*). This is one of the most colourful and popular of our flowering Eucalypts and the colour and size of the blossoms of the Chiddarcooping trees surpass anything I have seen elsewhere – cultivated or otherwise.'

Shugg then penned a pivotal letter for the Chief Warden of Fauna to the Under Secretary for Lands dated September 7th 1960;

> *'Re Reserve 19210 and adjacent Crown land*
>
> *Further to our previous correspondence, I am pleased to advise that an inspection of the above area has been made by an officer of this Department and the Superintendant, Forests Department.*
>
> *I concur completely with the sentiments expressed by Mr Brockway, a copy of whose memo is attached and also of those expressed by the Conservator in his memo to you dated December 16.*
>
> *I understand that the granite outcrops extend well into location 372 and it would seem most inadvisable to alienate it. Wherever the granite outcrop does occur land cannot be cultivated and is of very little use to agriculture.*
>
> *I am informed that this must be one of the outstanding areas of its kind and that it might well become an important national park. I strongly recommend therefore that the whole of the area bordered red on the accompanying sketch, including the existing reserve on location 373 be set aside as a reserve for "water and conservation of flora and fauna" and vested in the Fauna Protection Advisory Committee.'*

This submission was ultimately successful, with some inbuilt delay because Yilgarn Location 372 to the west of Chiddarcooping reserve was held as a special lease by WC and DM Carrod until December 31st 1969, after which consideration for its addition to the reserve was proposed by the Under Secretary for Lands. In the meantime, on December 7th 1960, Governor Charles Gairdner assented to a doubling of the size of Chiddarcooping reserve to *ca* 2610 ha, adding substantial areas of granite outcrops to the west of Chiddarcooping Hill as far as the east flank of the major north-south creekline (Fig 1), as well as extensive yellow sandplain and lateritic uplands to the north.

This did not stop applications for agricultural use, however. The Under Secretary for Lands wrote to the Chief Warden of Fauna on November 19th 1964 indicating that an application had been received for the portion of Flora and Fauna Reserve 19210 north of the future Morrison Road (location 1428), and asking if there were any objections. A terse reply, penned on November 27th by Shugg on behalf of the Chairman of the Fauna Protection Advisory Committee stated: 'This is an outstanding area not duplicated elsewhere in any other reserve of its type, and I am quite opposed to any part of it being removed from the control of my committee.'

Surrounded by new farms

Incremental land clearance essentially isolated Chiddarcooping Nature Reserve from other areas of native vegetation. By 1968, all of the reserve's eastern boundary and most of the southern block abutted cleared farmland, with similar agricultural landuse rapidly approaching other boundaries. As the number of surrounding farms increased, the issue of access to neighbours and roads through the reserve became important to the local community.

A significant proposal influencing the northern part of the reserve emerged in a letter of April 28th 1972 from the Under Secretary for Lands to the Director of Fisheries and Fauna, requesting views on a proposal from the Shire of Westonia seeking protection of a reserve to extend Morrison Road east-west through the Chiddarcooping Flora and Fauna Reserve. For reasons unclear in archival material, a reply dated July 25th 1972 raised 'no objection ... provided the protected road runs along the southern boundary of location 1428.' Agreement to this roadworks proposal is puzzling given the strength of earlier correspondence protecting the reserve's boundaries and biodiversity values. Perhaps a narrow road reservation was regarded as a relatively small but important concession to local community needs compared with agreeing to applications to alienate larger sectors of the reserve for agriculture.

In any event, some local attitudes to Chiddarcooping became apparent two years later, after the Under Secretary for Lands wrote on December 11th 1973 to the Director of Fisheries and Fauna, requesting consideration for a proposal to reserve for the purpose of the conservation of flora and fauna Yilgarn Location 374 immediately south-west of the then existing Chiddarcooping reserve. Fauna Warden JE Neal from Wongan Hills conducted a field inspection and interviews on the matter late in January 1972. In his report, he noted:

'... interviewed Westonia Shire Clerk Mr D Marsh. ... he seemed perturbed that it was not going to be thrown open for selection. He said that a number of farmers in the area had not been able to expand further and he thought that this would give them the opportunity. He said he thought that there were quite enough reserves in the Shire and considered that block 374 as a Fauna Reserve would constitute a dangerous fire and vermin hazard particularly as it adjoined Chiddarcooping Hill Reserve.'

After reviewing his observations on flora and fauna, and in view of the discussion with the Westonia Shire Clerk, Fauna Warden Neal consequently recommended that

'... 374 would be an invaluable acquisition as a Fauna Reserve. However, its close proximity to the identical Chiddarcooping Hill Reserve, and the fire hazard involved should, I feel, be professionally considered in this instance.'

Chief Research Officer AA Burbidge was subsequently consulted, and supported the recommendation to accept the Under Secretary for Lands' offer of Location 374 as a nature reserve, adding the suggestion that it should be added on to Chiddarcooping Reserve rather than created as a new reserve on its own. This advice was conveyed in a letter to the Under Secretary for Lands dated March 15th 1974, who subsequently decided to enlarge Chiddarcooping accordingly, and also add the substantial granite outcrops west of Chiddarcooping Hill on location 372 now that the special lease held by W C and D M Carrod had expired. However, location 372 was split in two so that only its eastern rocky half (now location 1486) was added to the reserve, while the western half was made available for agricultural selection. Thus, by June 1974, the intention to enlarge Chiddarccoping Nature Reserve to its present size of 5262 ha (Fig. 1) was established, and relevant paperwork prepared. However, formal gazettal did not occur until four years later, on June 16th 1978.

The creation of the reserve occurred in a local context of agricultural expansion into marginal farming country. It was driven by State Government officials with an interest in nature conservation against the wishes of some local community interests. Such a controversial origin is a familiar story associated with the creation of other, but not all, conservation reserves at this time.

Fires and firebreaks

Fires undoubtedly had occurred at Chiddarcooping from the mid-late Tertiary onwards as Australia drifted north from Antarctica and rainforest was replaced by contemporary vegetation (Hopper *et al.* 1996). However, details of past fire regimes have yet to be investigated on the reserve, and recorded fire information is very recent. Government records of fire I have traced became a reality for the newly enlarged Chiddarcooping Nature Reserve on the 11th and 12th of February 1975. A large fire front from farmland to the west approached the northern sector of the west boundary of Chiddarcooping Nature Reserve either side of Morrison Road. Two new firebreaks each about a kilometre long were bulldozed through the reserve ahead of the fire on a north-south alignment off Morrison Road, but the fire stopped short of these as it ran into granite outcrop country and ran out of combustible fuel. On this occasion the fire ignition risk was clearly located on land alienated for agriculture, and the Nature Reserve served to protect other farmland through the extinguishment of the blaze.

In the mid 1970s, the Department of Fisheries and Wildlife successfully applied to Government for an increased allocation to construct new firebreaks on nature reserves in the wheatbelt. Some 1221 km of firebreaks had been constructed or planned up to June 1976 (Burbidge & Evans 1976), including nature reserves containing major granite outcrops such as Boyagin (144 km), Chiddarcooping (60 km), Mt Caroline (6 km), Tutanning (13 km), and Two Peoples Bay (35 km). Chiddarcooping's 60 km were put in place by November 1975, and included coverage of all external boundaries, both sides of Morrison Road, and north-south internal firebreaks bisecting the northern and southern blocks.

The mid 1970s was also the last period when attempts to sequester parts of the nature reserve for agricultural development occurred. On September 27th 1976, the local member of parliament wrote to the Director of Fisheries and Wildlife conveying a request from an adjacent landowner who desired to swap some rocky uncleared land on his property for part of the southern block of Chiddarcooping Nature Reserve. The Director subsequently refused this application in a reply dated January 25th 1977.

Class A status achieved

Detailed biological research on Chiddarcooping Nature Reserve commenced in June 1978, the same month when the present-day boundaries were formally gazetted. Together with Flora Wildlife Officer B Haberley, I, as a recently appointed Flora Conservation Research Officer with the Department of Fisheries and Wildlife, embarked upon a survey of known populations of *Eucalyptus caesia* (Plates 1, 2, 3) in the wheatbelt, visiting and mapping the species on Chiddarcooping during June 8th and 9th. A series of investigations on the conservation biology of this attractive pink-flowered rare mallee ensued, and is still ongoing (Hopper 1981; Hopper *et al.* 1982, 1985; Hopper & Burgman 1983; Moran & Hopper 1983; Rye & Hopper 1982). In 1978 the species was considered both rare and possibly endangered by commercial seed collection, so it was included under the first schedule of flora declared in 1980 as Rare under the Wildlife Conservation Act (Rye & Hopper 1981).

Ongoing work on *Eucalyptus caesia* brought me back to Chiddarcooping in successive years, and I began collecting other plants of interest. For example, the common inland wandoo trees on the reserve and elsewhere were researched in collaboration with CSIRO botanist Ian Brooker, and subsequently named as the new species *Eucalyptus capillosa* subsp *capillosa* (Brooker & Hopper 1991). The first collection of a large white-flowered scale-leaved triggerplant was also made. This was subsequently passed to geneticist Dave Coates for investigation, found to be a new species (Coates & James 1996; Coates 2000), and formally named as *Stylidium chiddarcoopingense* (Lowrie *et al.* 1999).

As part of a general review of the classification of nature reserves, the Senior Clerk Reserves Robert Powell wrote to me on June 9th 1982 seeking advice as to whether a request should be made for Chiddarcooping Nature Reserve to become Class A, which would mean that its purpose or boundaries could only be changed through agreement of both houses of parliament. I prepared an affirmative report based on my field notes and research data. The Department's submission of 22 June 1982 argued "Chiddarcooping Nature Reserve contains 54% (550) of the total number of known wild *Eucalyptus caesia* subspecies *magna* (or "silver princess"), and 26% of the total known wild plants of the species as a whole. It is the only reserve with subspecies *magna* on it other than Billyacatting Hill Nature Reserve, which has only 9 plants. Chiddarcooping Nature Reserve therefore is essential for the conservation of this valuable ornamental eucalypt, gazetted as rare flora." Other values of the reserve were highlighted, including the spectacular granite landscapes, the presence of many granite rock endemic plants and species at the margins of their geographical distribution, an outstanding honeyeater avifauna (Hopper 1981), and the likely presence of other rare plants.

After the Under Secretary for Lands determined that the Under Secretary for Works had no objections, the reserve was reclassified to Class A, its purposes reordered to "conservation of flora and fauna, and water", and vesting assigned to the Western Australian Wildlife Authority on October 11th 1983. It has remained with this classification subsequently, other than vesting presently being with the National Parks and Nature Conservation Authority, and day to day management is now the responsibility of the Department of Conservation and Land Management.

Preliminary biological surveys by Department of Fisheries and Wildlife staff for a proposed management plan were undertaken in 1982. Judith Brown and Andrew Williams collected plants, including the first record of an unusual relictual *Acacia* with terete net-veined phyllodes that was subsequently named as *A. lobulata* (Cowan & Maslin 1990).

Further significant advances in knowledge of Chiddarcooping's flora and vegetation arose when consultant botanist Arthur Weston was contracted by CALM's newly formed Planning Branch to undertake a detailed botanical survey as a baseline document for the proposed management plan. Weston (1985b) made collections and observations on five field trips between September 1984 and February 1985. He presented data in the form of vegetation maps, a species list, and paid special attention to identifying rare, restricted and otherwise significant species and communities. Weston identified 21 rare and geographically restricted plant species on the reserve.

In relation to fire, Weston recommended that 'best short-term fire management policy is to exclude fire until a detailed, well-researched, long-term management plan to preserve habitat, flora and fauna complexity is developed. Development of such a plan requires the accumulation and integration of more information about the reserve than is currently available.' Weston's survey occurred at a time when it had been many decades since fire had swept most of Chiddarcooping Nature Reserve. Within two years this would change for the central valley, and within 15 for the entire northern half of the reserve.

1978, 1987 and 2000 wildfires

Late in 1978 areas on the north-western boundary north and south of Morrison Road, and on the western side of the southern block were burnt by wildfire (Weston 1985b). The lack of fuel on granite outcrops stopped some of this fire front, but a new firebreak trending south-west was cut for the specific purpose of stopping the fire in the north-west sector of the reserve. This was the same area burnt in February 1975. The consequences for biodiversity of such a short interval between fires were unknown.

The November 1987 lightning strike led to much of the main central valley outcrops west of Chiddarcooping Hill being burnt (Fig 1). The ignition point was south-west of Chiddarcooping Hill, and the fire spread west and north-westwards up the main valley before being headed off by a combination of bare rock and a raked and bulldozed firebreak cut specifically across the main creekline and down its east flank to stop the fire (K Wallace, CALM, personal communication).

Most recently, Chiddarcooping Nature Reserve experienced another lightning strike near the southern boundary of the north block on January 7th 2000. An extensive fire then consumed the northern half of the reserve, including all the central granite valley area burnt in 1987. Once out of the granite outcrop country, the fire rapidly continued north into the uncleared private property encompassing Coorancooping Hill (P Roberts, CALM, pers comm). It was stopped by cleared farmland on the boundaries of the nature reserve and adjacent private property to the north, except for the area west of Chiddarcooping Hill where a firebreak was constructed through large granite outcrops and the blaze eventually extinguished. Other new firebreaks were cut into the reserve in the vicinity of Chiddarcooping Hill in attempts (some successful, some not) to head off the blaze.

This wildfire was the first in 25 years to realize farmer's concerns about the Nature Reserve being a source of ignition and risk to their land. However, the fire did not encroach beyond the boundaries of the nature reserve onto farmland, except to the north where uncleared remnant vegetation extended into private property. As with any fire, a range of opinions was considered in trying to secure control. Some suggested running grids of firebreaks through the reserve, but this was resisted by CALM staff concerned for biodiversity as well as for the effectiveness of such an intrusive measure. Some firebreak construction ensued, but the idea of an extensive grid was not adopted.

It is clear that data on the effect of fire regimes on biodiversity would materially assist management decisions relating to wildfire control. Biodiversity is the full range of living organisms and the processes that sustain them. So what is known of Chiddarcooping's biodiversity?

Biodiversity values

Chiddarcooping Nature Reserve has important biodiversity values, containing an unusually diverse array of possibly 600 species of vascular plants (Weston 1985b). As indicated above, a number of these were unnamed until recently, including common dominants such as inland wandoo (*Eucalyptus capillosa* subsp *capillosa* Brooker & Hopper 1991). Chiddarcooping Nature Reserve is the type locality for *Eucalyptus crucis* subsp *lanceolata* (Brooker & Hopper 1982), the relictual and critically endangered Chiddarcooping wattle *Acacia lobulata* (Cowan & Maslin 1990; Brown *et al.* 1998) and the Chiddarcooping endemic *Stylidium chiddarcoopingense* (Lowrie *et al.* 1999). There are several other rare, relictual or biologically interesting plants on the reserve (Weston 1985b).

The main plant communities in the reserve identified by Weston (1985b) are low forests, woodlands, mallee, kwongan shrublands and resurrection and herbaceous communities on granite. Resurrection communities include ferns, mosses, herbs and woody herbs or subshrubs that appear dead when dry but become green after rainfall. Rare communities include mallee stands dominated by *Eucalyptus caesia, E. petraea, E. stowardii* and *E. erythronema*. Inland wandoo *E. capillosa* subsp *capillosa* woodlands were also uncommon, and one with *Acacia lobulata* as understorey is unique.

Of the 530 plant taxa recorded by Weston (1985b), the largest genera were *Acacia*, with 35 species, *Eucalyptus*, with 19 species, and *Melaleuca*, with about 20 species. Chiddarcooping Nature Reserve is especially rich in plants, exceeded in the wheatbelt only by larger national parks such as Lesueur, Stirling Range, Fitzgerald River and Kalbarri, and by nature reserves at Tutanning, and the Wongan Hills.

Only 19 of the 530 plant taxa recorded by Weston (1985b) are weeds, a remarkably low number for a wheatbelt reserve. All 19 are annuals, and none occupied significant areas. This reflects the large size and relatively low level of disturbance experienced by Chiddarcooping Nature Reserve since the 1870s. Bulldozing an extensive grid of permanent firebreaks, removing the topsoil in the process, may significantly change this situation, opening the way for a much more substantial presence of weeds in the reserve. This has been the case for Kings Park, where excessive unplanned track and firebreak construction has exacerbated the weed problem (Anon 1995).

There have been a few intensive biological studies of plants at Chiddarcooping. Published work on *Eucalyptus caesia* subsp *magna* has already been mentioned (Hopper 1981; Hopper *et al.* 1982, 1985; Hopper & Burgman 1983; Moran & Hopper 1983; Rye & Hopper 1982). Ongoing studies of pollination ecology (Hopper & Wyatt, unpublished) have revealed fresh insights. For example, in the wild at Chiddarcooping, as well as in cultivation, *E. caesia* subsp *magna* has a range of nectar accessability features that are associated with more reliable honeyeater visitation and potentially greater movement among trees by honeyeaters than is seen in subspecies *caesia* at Boyagin Rock. *Magna* has fewer, larger, more widely dispersed flowers on any given day, treble the nectar available per flower per day, with continuous daily production, and daily sugar concentrations that remain low at levels preferred by honeyeaters.

Recent DNA studies of *E. caesia* by Margaret Byrne and Siegy Krauss are helping to resolve the evolutionary sequence of populations. Chiddarcooping's stands of subspecies *magna* may be derived from the nearby Yanneymooning Hill population of subspecies *caesia*, but have a large number of genetic differences in chloroplast DNA, signalling either a long period of independent evolution or very rapid evolutionary divergence.

Coates (2000) and Coates & James (1996) established similar significant genetic divergence of *Stylidium chiddarcoopingense* from its nearest relative *S. nungarinense*. Moreover, the relictual status of *Acacia lobulata* has recently been confirmed using DNA markers by Margaret Byrne and colleagues (CALM, personal communication).

Chiddarcooping's well-watered south-facing slopes flanked by large granite outcrops appear to have been important habitat enabling the persistence of species for very long periods of time during the climatically turbulent late Tertiary and the Pleistocene ice ages (Hopper 1979, 2000; Hopper *et al.* 1996). Harry Shugg's prediction that Chiddarcooping would become an important National Park has been borne out as research on its biodiversity continues.

A comprehensive survey of the fauna, fungi, cryptogams and other biodiversity of Chiddarcooping Nature Reserve has yet to be undertaken. A start was made in the mid 1980s in anticipation of a proposed management plan (S Moore, CALM, personal communication), but this project was deferred in the face of other priorities. Based on discoveries already made on the flowering plants, it is highly probable that the reserve will yield rare, relictual and otherwise significant invertebrates and other organisms when adequately surveyed.

Plant responses to the 1987 fire

The 1987 wildfire consumed a stand of *E. caesia* and presented an opportunity to examine recruitment after fire of this and associated species of granite outcrops. Weston's (1985b) recent survey of the flora and vegetation of Chiddarcooping Nature Reserve provided a useful and thorough benchmark for the prefire plant communities.

A total of eighteen 10 m x 1 m permanently marked transects were established to monitor postfire regeneration (Fig 1). The transects were placed on areas with the densest seedlings of *E. caesia* subsp *magna*, *E. crucis* subsp *lanceolata*, and *E. petraea*, to maximise information on mallee eucalypt recruitment and seedling survivorship, as well as in representative areas of other common granite outcrop species such as *Allocasuarina huegeliana* (Plate 4), *Hakea petiolaris*, *Thryptomene australis* and *Borya constricta*. In addition, some transects were established across the bulldozed and raked northern firebreak and adjacent spring-burnt bulldozed spoil heaps (Plate 5) to track regeneration of plants and compare this with adjacent undisturbed plant communities burnt by the wildfire.

A total of 129 species were recorded in the 18 transects, 28 of which were not listed among the 530 taxa for Chiddarcooping Nature Reserve by Weston (1985b). This represents a 22% increase in taxa recorded for the granite outcrop communities on the reserve. Of the 28 new records, 15 were annuals, 10 were perennial shrubs (including 5 legumes), and three were short-lived postfire opportunists such as *Gyrostemon subnudus*. One legume, *Gompholobium marginatum*, was found to represent a significant inland range extension based on herbarium records. The blue china orchid *Cyanicula ashbyae*, described recently (Hopper & Brown 2000), was recognised as new to science for the first time in 1978 when found at Chiddarcooping. Clearly, fire on wheatbelt granite outcrops reveals hidden and sometimes unexpected biodiversity.

The transect study established the presence of high floristic complexity over short distances, a well known feature of granite outcrop vegetation (Hopper *et al.* 1997). Species richness was highest in the *Borya-Thryptomene* transect (54 taxa, mainly annuals), and lowest in the spring-burnt spoil heap (10 taxa). The most common species found in the 18 transects after wildfire included;

Allocasuarina campestris (16 of the 18 transects)
Acacia lasiocalyx (15)
Gyrostemon subnudus (15)
Calothamnus quadrifidus (14)
Dampiera haemotricha subsp *dura* (14)
Glischrocaryon aureum (14)
Acacia restiacea (13)
Grevillea paniculata (13)
Spartochloa scirpoidea (13)
Billardiera erubescens (12)
Lepidosperma viscida (12)
Thysanotus dichotomus (11)
Vulpia myuros (11)
Melaleuca macronychia (11)
Pentaschistis airoides (11)
Eucalyptus crucis subsp *lanceolata* (10)
Dodonaea viscosa subsp *spathulata* (10).

There are several interesting aspects to this list of common species. Firstly, as documented by Weston (1985b) for the whole reserve, weeds are few (only the two annual grasses *Vulpia myuros* and *Pentaschistis airoides*). Normally, wheatbelt granite outcrop herbfields are replete with weed species, constituting up to 20%+ of all taxa (Ornduff 1987; Ohlemueller 1997). The large size of Chiddarcooping Nature Reserve and the central location of the transects on the reserve may explain its remarkably low weed numbers.

Secondly, only 5 of the 15 most common native species are resprouters capable of regenerating from underground buds off lignotubers or rhizomes (*i.e. Glischrocaryon aureum, Spartochloa scirpoidea, Lepidosperma viscida, Melaleuca macronychia* and *Eucalyptus crucis* subsp *lanceolata*). The majority of species are woody seeders, killed by wildfire and regenerating only from seed stored in the soil or in their canopies.

Indeed, looking at all 129 species found in the transects, 86% are seeders and only 14% are resprouters at Chiddarcooping. Even deleting the 50 annual species and focussing only on the 79 perennials, 77% are still seeders compared with 23% resprouters. This is in marked contrast to many other plant communities in south-western Australia, where the proportions are reversed with around one third of the species are seeders and two thirds resprouters. Some frequently burnt south coastal communities such as at Two Peoples Bay Nature Reserve east of Albany have only 8% seeders and 92% resprouters (AJM Hopkins, CALM, personal communication), while Bell (1985) found 34% seeders and 66% resprouters among 152 species from the Badgingarra-Jurien kwongan. Bennett (1987) found in mallee communities of the Ravensthorpe Range that 42% of species were seeders and 58% resprouters. Hassell (2000) recorded 51% seeders and 49% resprouters among 277 species of mallee and banksia shrublands in the Fitzgerald River National Park. Van der Moezel & Bell (1984) came closer to or exceeded the Chiddarcooping situation in a study of communities north of Esperance, recording between 61-100% seeders and 29-0% resprouters at seven different sites.

The dynamics of Chiddarcooping granite outcrop communities following wildfire show predictable patterns. Greatest species richness is seen in the first year following fire, and declines steadily thereafter (Plates 1, 2, 3). For example, many of the 50 species of annuals in the transects were only seen in the 1988 winter-spring (except for the open *Borya-Thryptomene* community, where annuals persisted over several years). The orchid *Cyanicula ashbyae* (Hopper & Brown 2000) flowered only in that same spring and was not seen in subsequent years, although undoubtedly it was present as underground tubers. *Gyrostemon subnudus* declined from one of the most common species in the first year after fire to a few straggly survivors by the third year.

Resprouters and seeders displayed different seedling recruitment patterns, exemplified by *Eucalyptus crucis* and *Allocasuarina huegeliana* respectively (Fig 2, Plate 4). Even though an average of 10 seedlings per square metre was recorded for the mallee *E. crucis* in 1988, this declined to just one by the next year, and all had died by three years after the 1987 wildfire. Canopy cover for this species' transect developed rapidly from annuals and lignotuberous resprouts over the first two years, then thinned and gradually increased again as leader shoots of *E. crucis* started to dominate. Flowering off resprouting shoots occurred within 18 months for *E. caesia*, and within three years for *E. crucis*.

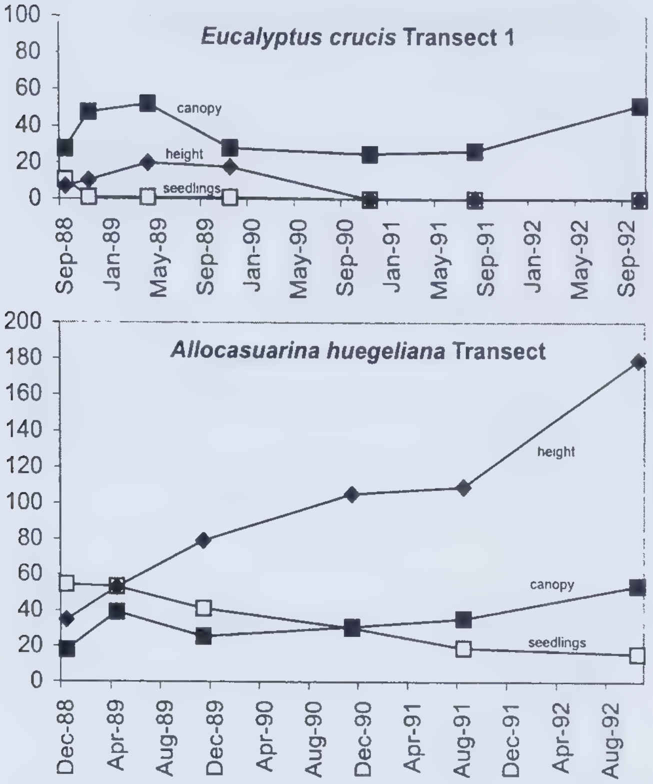


Figure 2. Projected canopy cover, number of seedlings per square metre and mean seedling height in 10m x 1m transects for *Eucalyptus crucis* subsp *lanceolata* and *Allocasuarina huegeliana* in granite outcrop vegetation at Chiddarcooping Nature Reserve following a wildfire in November 1987.

Rock sheoak or Kwowl (*Allocasuarina huegeliana* – Plate 4), in contrast, produced seedling densities approaching a mean of 60 per square metre in the first postfire year, and declined gradually to 20 some four years later. Seedlings had grown to a mean height of 1.8 m by this time, but fruiting had not occurred to any significant extent until 9 years after the fire, and even then, seedlings were averaging only about 3-4 m in height. The need for a considerably longer period of time to elapse before a reasonably sized seed bank develops is evident at Chiddarcooping. Moreover, Muir (1985) showed that *Allocasuarina huegeliana* may successfully regenerate in the absence of fire. It is not essential to burn vegetation for recruitment of this obligate seeder.

In relation to regeneration on the bulldozed spoil heaps and raked firebreak, a striking difference was evident within three years of the 1987 wildfire (Fig 3). The plant community on the firebreak, which had only been raked by a bulldozer as a deliberate policy to leave the soil intact and minimise soil in push heaps (K Wallace, CALM, personal communication), recovered in a comparable if not more vigorous fashion to adjacent undisturbed communities. In contrast, most of the spring-burnt spoil heap showed little or no regeneration. It had been effectively sterilized. This situation prevailed for the next two years (Fig. 2), and, indeed, for at least 9 years after the fire (Plates 5, 6). Similarly, firebreaks bulldozed in 1975 with their topsoil removed show extremely slow rates of recovery when left abandoned. Raking and leaving the topsoil intact on temporary firebreaks is very much a preferred option in terms of achieving rapid recovery of native biodiversity.

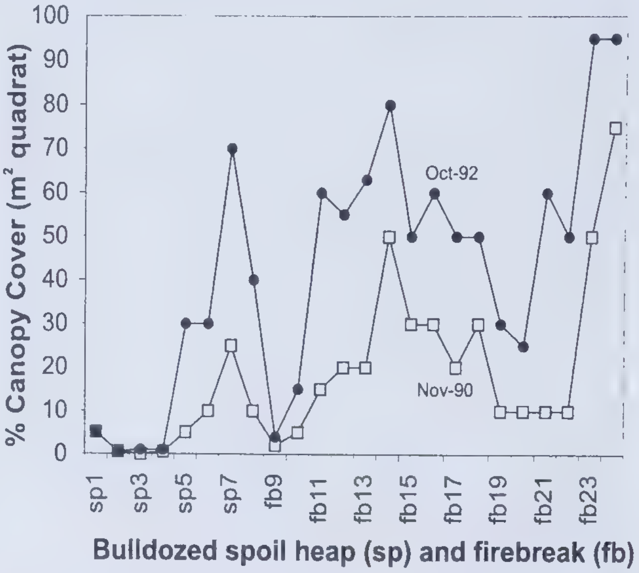


Figure 3. Projected canopy cover in 1m x 1m quadrats in a line transect from a bulldozed spoil heap burnt in spring 1988 across a raked firebreak through granite outcrop vegetation at Chiddarcooping Nature Reserve following a wildfire in November 1987. The prefire vegetation was a dense tamma (*Allocasuarina campestris*) and *Melaleuca uncinata* thicket.

Conclusions

It is important to emphasize that the detailed Chiddarcooping study relates to only one fire event at one location. Generalizing from such a low sample size needs to be treated with caution. What can be said, however, is that the hypothesis that granite outcrops provide refuge for fire-sensitive species is supported – Chiddarcooping granite outcrop communities have a remarkably high proportion of obligate seeder species that are fire-sensitive. Perhaps the refugial opportunities provided by the granite landscapes of Chiddarcooping account for the unusually high number of rare species documented for the reserve. Investigations of the life histories of these species would shed some light on this hypothesis.

Although the study tracking post-fire regeneration has covered barely a decade, it is clear that for some species of obligate seeders, intervals between fires measured in decades are likely to be required to ensure an adequate seed bank is available and local extinction is averted. The more recent wildfire in January 2000, which burnt over communities consumed in the November 1987 fire, provides a good opportunity to test this hypothesis.

For managers, this small study suggests that fire should be used with considerable caution on wheatbelt granite outcrops. Imposing a regime of regular prescribed burning without knowing recovery times for fire sensitive species could pose considerable risk to biodiversity on granite rocks.

Protection from fire seems the best strategy on present information where native vegetation persists on granite. Where firebreaks are intended to be temporary, they should be raked with the topsoil left intact because of the rapid recovery of native vegetation with reduced erosion that follows. Permanent firebreaks, with topsoil removed by bulldozing or grading with a blade are extremely slow to regenerate when no longer required in many communities. Hence their extent and location should be carefully considered.

Burning bulldozed spoil heaps may sterilize soil seed supplies. It would be preferable to spread such heaps over greater areas, and leave them unburnt if this is a practical option, as they provide habitat for fauna and decomposers such as fungi.

On granite outcrops completely denuded of native vegetation, and where the soil remains intact, a fire might stimulate some regeneration of soil-stored native plant seed. However, adequate weed control measures would need to be in place, and fire should not be used on a recurrent basis following the initial attempt at a regeneration burn. Alternatively, smoke dissolved in water could be applied, obviating the need to burn to stimulate germination (Roche *et al.* 1997a, 1997b, 1998). Working cautiously, on small areas, with an experimental approach, is advocated because we have so much to learn about fire and its impact on biodiversity. A wider examination of fire and its management on granite outcrops is needed to rigorously test some of the ideas presented above.

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Managing tourism and recreation on Wheatbelt granite outcrops

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Abstract

The conservation estate in the Western Australian wheatbelt is largely biased toward small remnants featuring either granite outcrops or salt lakes. Due to the high level of clearing for agriculture, these areas provide the primary resource for recreation in the natural environment. Although few sites receive more than 1 000 visitors per year, recreation impacts on natural and cultural values can be considerable. Potential recreational impacts on granite outcrop reserves include changes to soil structure, hydrology, vegetation, fauna, heritage and aesthetic values. These may be exacerbated by factors external to the reserve and the small buffer areas surrounding many granite outcrops.

Impacts associated with low level but widespread use of remnant vegetation were the subject of a study in CALM's Merredin District. Sixty sites managed by various agencies were surveyed with the aim of (a) identifying those most appropriate for recreation and tourism and (b) liaising with the relevant agencies over future development and management. Each site was ranked for recreation/tourism suitability by assigning numeric values to physical attributes, threats and uses, and current and future management. The study recommends concentrating development and management effort within the top 21 sites, and restricting recreation on the remainder. Several authorities have used the results of the study to support funding applications for recreation development.

Keywords: granite outcrops, recreation impacts, wheatbelt, management, habitat alteration, assessment

Introduction

The Western Australian wheatbelt is typical of other agricultural regions throughout the world, in that it has been largely cleared (93% in the central wheatbelt; Beard & Sprenger 1984) and flora and fauna persist primarily within small Crown reserves. The Wheatbelt Region of the Department of Conservation and Land Management (CALM) encompasses much of this area; the 'Wheatbelt', 'Wheatbelt Region' or 'Region' refer to CALM's Wheatbelt Region. Forty-three local government authorities (LGAs) have their administrative boundaries wholly or partly within the Region.

There are over 6 300 Crown reserves within the Wheatbelt. Fifty-five per cent are under five hectares, and 72 per cent less than 20 hectares. Approximately 2 500 are unvested (*i.e.* they have no managing authority), the Water Corporation, the Waters and Rivers Commission and LGAs manage approximately 3 100, and CALM manages 625. Most CALM-managed reserves are vested in the National Parks and Nature Conservation Authority (NPNCA) as nature reserves with a purpose of conservation of flora and fauna. The *Wildlife Conservation Act* (1950) and *Wildlife Conservation Regulations* (1970) provide the enabling legislation for the management and control of nature reserves. The legislation excludes most recreation activities, including camping and lighting fires in other than designated fireplaces. CALM's Recreation and Tourism Policy Statement provides further guidelines on the appropriateness of recreational activities on nature reserves.

Nature reserves in the Wheatbelt Region are heavily biased towards granite outcrops, lateritic breakaways, and salt lakes and associated habitats. Median reserve size is only 114 hectares, which exposes remnants to external influences such as increased radiation, wind and water fluxes, and chemical drift from farmland (Saunders et al. 1991). These impacts are exacerbated by the use of the reserves for recreation. Local people, who have little opportunity for 'natural' recreation experiences on private property, are the main users (Plate 1), although some tourism also exists. Recreation and tourism are often used synonymously to describe leisure activities taken for pleasure and personal satisfaction (Pigram 1983). A commonly used definition to distinguish between them is that a tourist is a recreationist who has traveled more than 40 kilometres and stayed overnight away from his or her normal place of residence. In terms of environmental impact, there is very little difference

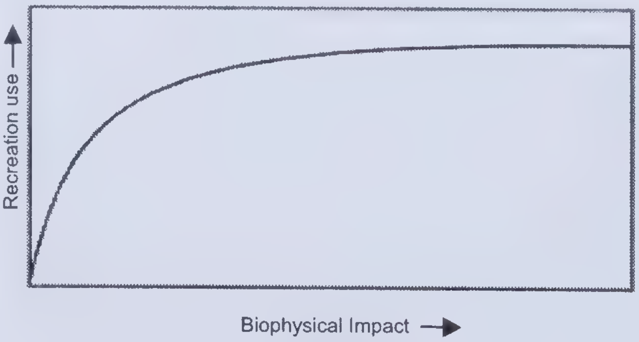


Figure 1. Visitor use *vs* level of impact (modified from Hammit & Cole 1987, and Cole 1993).

between the two. The main tourism attraction in the Wheatbelt is Wave Rock near Hyden, which attracts in excess of 100 000 visitors per year to view the unusual rock formation. CALM is also supporting a feasibility study of a tourism attraction based on black-footed rock wallabies (*Petrogale lateralis*) in the Wheatbelt. Although most reserves are subject to only low levels of recreation (mainly picnicking), the fragility of granite outcrop ecosystems in particular has led to significant degradation at many sites.

The effects of recreation on natural areas

Relatively few sites in the Wheatbelt receive more than 1 000 visitors per year (Moncrieff 1996). However, the level of impact upon natural, cultural and aesthetic values is not necessarily proportional to visitor numbers or the length of time a site has been used. Hammitt & Cole (1987) and Cole (1993) described the biophysical impacts of increasing visitor numbers over time, and found that even small increases in use could have a pronounced effect when visitation rates were low (see Fig 1). This should not, however, be considered in isolation; the timing, location, and type of use are also critical (Lindberg *et al*. 1996).

Cole (1993) described the impacts of recreation on four elements of natural systems, soils, vegetation, fauna and water. To this must be added cultural values, including Aboriginal and non-Aboriginal heritage, aesthetic quality and recreation itself. Impacts to these elements are described in general terms below, with specific reference to Wheatbelt granite outcrops.

Natural values

Soils

Soil can be affected by pedestrian, vehicular and animal traffic (*e.g.* horse-riding). Trampling causes soil compaction and loss of the organic surface layer, necessary for biological activity and water absorption (Cole 1993). Preservation of the organic layer is extremely important for a number of reasons, *viz*;

- the role it plays in biological activity;
- it increases the absorptive capacity of the soil;
- it provides a source of nutrients for plant growth; and
- it is more resilient to erosion than underlying mineral soils.

Loss of the organic layer allows soil compaction which reduces the air spaces between soil particles and hence infiltration capacity (Monti & Mackintosh 1979). This, in turn, leads to reduced access to water and nutrients by plant roots, reduced seed germination, and loss of soil-dwelling biota (Cole 1993). The latter play an important role in the development of soil structure and nutrient cycling. Vegetation loss, soil compaction and loss of infiltration also increase surface water runoff and hence erosion potential. This is a particular problem on thin, poorly structured soils found around the base of granite outcrops (Plate 2).

Vegetation

The vegetation of a typical Wheatbelt granite outcrop has been described by Piggot & Sage (1997) for Yilliminning Rock. They described seven vegetation associations, including Low Woodland and Woodland supporting wandoo (*Eucalyptus wandoo*) and salmon gum (*E. salmonophloia*). These vegetation types are typical of better soils and have been extensively cleared for agriculture. Remnant patches of woodland associated with granite outcrops therefore contribute significantly to nature conservation (Withers & Edward 1997). However, woodland sites also tend to be favoured as sites for recreation, providing shade, scenic beauty, and firewood for barbecues (Plate 3). The small size of these remnants, the dominance of the granite massif within many reserves, and an often large perimeter to area ratio lead to woodland remnants being even more susceptible to external influences, such as weed invasion on soils disturbed by recreation.

Loss of vegetation is one of the most obvious signs of unsustainable site use. Informal access, firewood collection and wanton vandalism can all lead to decreased plant vigour, expressed through changes to plant biomass, composition, cover and structure (Plate 4). Visitors, vehicles and horses can also spread weed seeds (Buckley & Pannell 1990; Lonsdale & Lane 1991; St John Sweeting & Morris 1991) although in the Wheatbelt this is likely to be of minor consequence in comparison to weeds invading from adjoining agricultural land. Of greater concern is dieback, a soil-borne fungus (*Phytopthora* spp) spread by water, pedestrians and vehicles. Pedestrian and vehicle bans have been instigated in many sites in the wetter parts of the Western Australia (*e.g.* Stirling Ranges). The low rainfall in the Wheatbelt is generally not conducive to dieback, although granite outcrops may be susceptible due to their water-gaining capacity. For example, dieback has been recorded at Moorine Rock, 80 kilometres east of Merredin (Hussey 1997).

The diversity of microhabitats on granite outcrops has led to a high level of floristic endemism. Hopper *et al.* (1997) found 16% of orchids and 24% of eucalypts on south-western granites were endemic. Granites also contribute 32 taxa (9.8%) to the State's threatened flora list (Brown *et al.* 1998).

Fauna

Cole (1993) described the manner of impacts on wildlife as either consumptive (*e.g.* hunting or fishing) or non-consumptive. Non-consumptive impacts include;

- habitat modification
- pollution/littering; and
- direct disturbance when recreationists approach too close to wildlife.

In a review of 166 cases of non-consumptive human-wildlife interactions, Boyle & Samson (1985) determined 82 per cent of impacts were negative. The most damaging pursuits were off road vehicle use (95% of studies), hiking and camping (79%) and wildlife observation and photography (74%). The latter result is interesting, as wildlife observation and photography are commonly thought of as relatively benign pursuits. Knight & Cole

Plate 1. Farmhouse adjacent to granite outcrop. Rocks such as this provide the main natural recreation areas for many wheatbelt families.

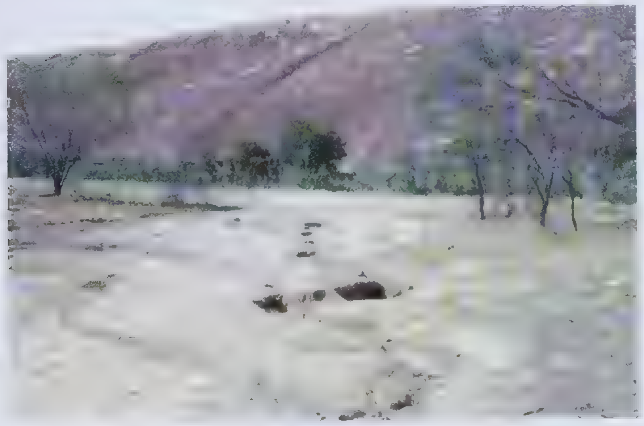


Plate 2. Erosion caused by vehicle traffic, Yorkrakine Rock.

Plate 3. Picnic site typical of many granite outcrops throughout the wheatbelt. Yilliminning Rock.

Plate 4. A carpark at Yorkrakine Rock, an area once covered by Jam (*Acacia acuminata*) woodland.

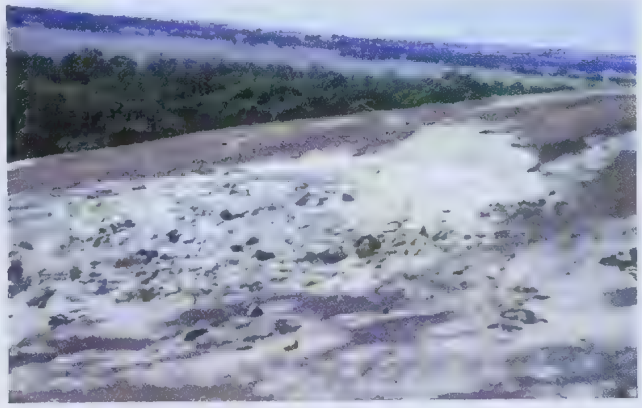


Plate 5. Exfoliated granite sheets smashed by visitors, Yilliminning Rock.

Plate 6. Rock-covered gnamma near Narrogin.

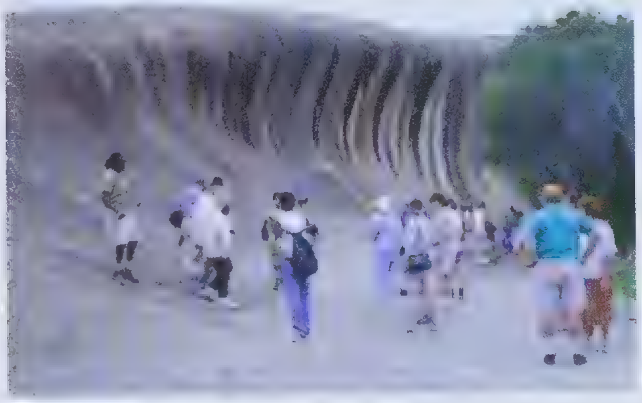


Plate 7. Rock catchment wall at Wave Rock, a common sight on many wheatbelt granites.

Plate 8. Graffiti at Yorkrakine Rock.

(1995) identified the very nature of the activity as potentially damaging; avid wildlife watchers and photographers seek out rare or charismatic species, often at sensitive times of the year (*e.g.* breeding), and actively approach animals for better photographs.

Habitat modification includes loss of vegetation required by animals for food, shelter or nesting, or the creation of artificial barriers to small wildlife (*e.g.* walking tracks). An excellent example of the problems associated with littering is provided by the former black-footed rock wallaby colony on Kokerbin Rock near Kellerberrin (WA). Kinnear (CALM, pers comm) found that captured animals invariably had cut feet from broken glass.

Direct disturbance to wildlife is usually only temporary, and animals return within several hours. However, there may be a major impact when animals are living under stressful conditions. Permanent relocation of large mammals has been documented for some North American species (Geist 1978, cited by Cole 1993), and could potentially happen to the isolated rock wallaby colonies on central wheatbelt granite outcrops if visitors are allowed random access.

The two main existing recreational impacts on Wheatbelt granite outcrop fauna are;

- the wanton destruction by visitors of exfoliated granite sheets around granite outcrops (Plate 5). These are often smashed into smaller pieces, and occasionally used to construct cairns on outcrop summits. Intact sheets provide habitat for numerous reptiles; and
- habitat loss through the combined effects of soil compaction, shrub loss and firewood collection in woodlands.

Withers & Edward (1997) described the terrestrial fauna of granite outcrops in Western Australia. Although few species were restricted to granite outcrop habitats, many species were found to use them. They reasoned that granite outcrops were important as seasonal resources or temporary refuges for the fauna of surrounding habitats, and urged the conservation of the ecotone between the granite outcrop itself and the surrounding habitats

Water

The distribution and quality of water can be impacted by recreation, most commonly by addition of pollutants/ nutrients through toilet wastes and washing, increased runoff and erosion from compacted soils, and deposition of sediments into waterways (Anderdeck 1994; Buckley & Pannell 1990). While the impacts of the latter two processes tend to occur as part of a process over time, pollution or fouling of gnammas can be instantaneous. Particularly susceptible is the aquatic vegetation and invertebrates found in gnammas, including one taxa of Declared Rare Flora. For example, Bayly (1992) attributed the high pH of one gnamma to the cement mortar used in rock wall construction to raise the level of the pool. A simple act such as bathing with soap could have a profound impact by altering nutrient balances.

Cultural values

Aboriginal Heritage

Bindon (1997) provided an excellent summary of the significance of granite outcrops to Aboriginal people. Granite outcrops provided hunting and gathering opportunities, religious and ceremonial use, and art sites. Gnammas provided an indispensable source of water, permitting occupation of otherwise inhabitable country. Covering gnammas with flat sheets of exfoliated granite protected water from evaporation (Plate 6; Mountford 1976, in Bindon 1997)

Outcrops also provided opportunities for hunting and gathering unavailable elsewhere. One of the most obvious examples is the lizard fauna common to outcrops. Bindon (1997) mentions evidence of 'lizard traps' on a number of south-west granites, although he concedes the function of these traps cannot be confirmed.

The significance of granite outcrops to Aboriginal religious beliefs and art can be demonstrated by using the example of Wave Rock. A dreaming story tells of an evil spirit woman who stole Aboriginal children to feed to her husband, Mulka. Mulka lived in what is now called Mulkas Cave near Wave Rock, leaving evidence of his existence through the handprints found on the ceiling of the cave. When the spirit people tried to stop the evil spirit woman from stealing the children, she leapt into the sky with the help of Hyden Rock, which was soft and acted as a trampoline (Morrison *et al.* 1993).

The significance of granite sites in dreaming stories led to their frequent use for ceremonial purposes. Stone arrangements, utilising slabs of exfoliated granite or other weathered products, often mark the sites. Unfortunately, they are very prone to vandalism and can be destroyed by simply shifting the stones. The integrity of lizard traps and rock-covered gnammas can similarly be destroyed. Aboriginal artwork can suffer a similar fate through carelessness or deliberate vandalism. In Hippos Yawn near Wave Rock, artwork on the ceiling of shelter was vandalised by graffiti. In removing the offending graffiti, Aboriginal hand stencils were also sandblasted off. Some of the hand stencils in Mulkas Cave are close enough for visitors to touch and, despite interpretive and warning signs, could easily be vandalised.

Non-Aboriginal heritage

Many Wheatbelt granite outcrops have been used as a source of water by explorers and for agricultural settlement. These take the form of wells and rock-walled catchments that channel rainfall runoff from the bare rock surface into catchment dams. Wells dug at the base of granite outcrops along natural drainage lines are common throughout the Wheatbelt (*e.g.* at Kokerbin Rock, Totagin, and Korrelocking). These features were often covered to reduce evaporation and fouling by animals. However, their integrity is often threatened by vandalism from visitors; invariably rubbish and timber is thrown in, and the fabric around the top of the wells, including the covers, is damaged.

Granite outcrops and their rock-walled catchments were the primary source of water almost all Wheatbelt towns. Perhaps the best known of these in Wave Rock, where the wall runs along the top of the 'wave' itself

(Plate 7). Although damage from recreationists at such a public site is unlikely, a small disused catchment at nearby Graham Rock has been largely destroyed. Other disused catchments have been similarly treated.

Aesthetic values

Limited research is available on the attractiveness of Wheatbelt landscape features. Stuart-Street & Kirkpatrick (1994) described the Wheatbelt landscape as being characterised by pastoral fields, expanses of cereal crops and wide open views, often unobstructed by remnant vegetation. Areas of highest scenic quality included;

- major rock outcrops;
- vegetation with a diversity of species, height and density;
- strong form, colour and texture contrasts with surrounding landscape (*e.g.* clumped remnant vegetation);
- distinctive stands of vegetation with strongly defined growth habits, texture and colour (*e.g.* Salmon Gum and other woodlands); and
- dramatic displays of seasonal colour.

All of these landscape components are common features of granite outcrops and their surrounds, reinforcing the importance of granite reserves as a major contributor to aesthetic quality in the Wheatbelt. However, their prominence, fragility, common use for recreation, and the familiarity of local people to site detail mean that visual quality can be easily diminished. For example, a yellow rubbish bin on top of one granite outcrop near Bruce Rock is visible from the surrounding countryside for over a kilometre. Vehicle tracks on moist soil on outcrop aprons can leave a visual scar lasting for decades. Graffiti is even longer lasting, as evidenced by that accumulated over many years at Yorkrakine Rock near Kellerberrin (Plate 8).

The retaining walls built to divert water for storage are common visual scars on many Wheatbelt granite outcrops. The best known of these is at Wave Rock. The impacts of such walls are threefold;

- they reduce visual quality;
- walls are typically constructed using exfoliated granite, reducing animal habitat; and
- the hydrological systems on granites are altered, potentially impacting on vegetation associations and animal habitats.

Conversely, the water catchment systems have played a vital part in the development of the Wheatbelt and even where no longer functional, retain heritage value.

Reducing the impacts

It is acknowledged that, apart from the tourism industry associated with Wave Rock, most sites are used by local people. This poses a particular problem for managers in determining whether sites are used primarily because of their proximity, or their features. Herbert & Schmidt (1982), in a survey of visitors to the Darling Plateau forest to the immediate west of the Wheatbelt, found that;

- 46% of those surveyed chose a particular site due to its landscape amenity and site features;
- 9% for the activities they could undertake;
- 17% for psychological or social reasons; and
- 22% for the facilities present.

The last category was further subdivided into seven criteria, including accessibility and availability and type of facilities present. Of responses in this group, 61% (or 13.6% of the total surveyed) considered the availability of facilities to be paramount, whereas only 20% (4.4% of the total surveyed) rated access as most important. If these findings apply to the Wheatbelt, it is possible that although current use may be due to a site's proximity to the local population, use would decrease if additional facilities were provided elsewhere. For example, providing picnic facilities and a greater level of visual amenity may attract visitors to a centralised location. Such sites could be 'hardened' and managed to prevent further deterioration. However, consideration must be given also to the 'friction of distance' concept: that is, sites at a greater distance, or perceived as involving more time, effort or cost to get to, are patronised less (Pigram 1983).

Site hardening and management techniques include;

- using barriers to restrict access;
- banning campfires, or alternatively providing firewood and fire rings, or gas/electric barbecues;
- interpretation and information on recreation impacts and site features;
- provision of toilets;
- forming, surfacing and maintaining roads and pedestrian tracks to prevent erosion; and
- seasonal site closures.

McArthur & Hall (1996) recognised that hardening could compromise the heritage values of sites by failing to blend with the surrounding environment. Sensitive design can help to overcome the obtrusiveness of many hardening and management techniques. For example, the use of site topography and natural vegetation as visual screens, and using appropriate local materials and colours for facilities and signage can reduce visual impacts.

One management response: targeted development

The distribution and number of reserves, and the low-level recreation associated with most, has proven problematical for managers and has led to varying degrees of degradation. In 1995 the Wheatbelt Region of CALM initiated the preparation of a recreation and tourism plan for the Merredin District with the following goals;

- to maximise the diversity of recreation opportunities whilst rationalising recreation use of reserves, and hence preventing further degradation of conservation, cultural and aesthetic values;
- to provide a focus for provision of tourist and recreation services and information;

- to provide additional tourist income to the region by attracting transient traffic, and encouraging current visitors to stay longer; and
- to initiate mutually beneficial partnerships with LGAs in regard to recreation and tourism activities.

Although it is acknowledged there are many techniques available to managers to reduce impacts (including education, enforcement, temporal and spatial zoning), it was reasoned that these goals could be best achieved by concentrating use and management at selected, hardened sites. The reasons for choosing this management response was twofold; (1) due to the lack of resources needed to implement other strategies, and (2) to involve LGAs in determining priorities for development, and their ongoing management. An integral part of the planning process was the consideration of recreation resources on all Crown Reserves, including sites managed by CALM as well as other authorities such as LGAs. Consequently, collaboration with LGAs to identify potential sites, and ensure satisfaction with the process of ranking sites for development, was a high priority.

Methodology and site assessment

A four part process was devised to meet project goals. Firstly, letters were sent to the 16 LGAs within CALM's Merredin District in November 1994, requesting information on any nature-based recreation/tourism sites managed by authorities other than CALM. A standardised format for recreation site assessment was then developed. Due to the large number of sites throughout the District and the distances between them, it was considered improbable that a single officer would be able to assess all sites. Standardising assessment procedures would allow results to be compared sites were assessed by different officers. The third step was to determine the most important criteria for assessing recreation and tourism potential. A scoring system was developed that divided the assessment into three categories, physical attributes (possible 100 points, or 57% of the total), threats and uses (possible 30 points, 17%), and current and future management (45 points, 26%). The proportion of the total score of each category was considered to represent their relative importance to future recreation and tourism activities, and although the category scores are somewhat arbitrary, the method still allowed a comparative analysis of sites. Lastly, a system was devised that enabled reserves to be ranked according to objective criteria.

Physical attributes

This category was divided into five criteria;

- proximity to a recognised travel route (maximum 20 points);
- proximity to services, such as fuel and food (maximum 10 points);
- site accessibility (8 points for 2WD, maximum 10 points for caravans)
- proximity to another type of feature (maximum 10 points); and
- natural attributes, including eight sub-criteria (maximum total 50 points).

The points assigned for the first two criteria acknowledge the importance of major travel routes and town services to site development. It was felt that these criteria provided the bases for recreation/tourism infrastructure in the study area. Subsidiary to this was the need to provide 2WD access, and to a lesser extent access for caravans.

Proximity to another type of site was also considered important. The majority of reserves in the Wheatbelt are based around granite outcrops or waterbodies. The provision of a diversity of site types was considered critical in maximising visitor interest. For example, a site consisting solely of a granite outcrop but with an area of waterbody within 10 km was awarded additional points.

Natural attributes contributed up to 50 of the 100 points allowable in the Physical Attributes category, and 29% of the total score. This acknowledges that the physical attractions of the Wheatbelt generally lack the scenic grandeur of other regions (*e.g.* the national parks to the south, the tall forests of the south and west, and the Pinnacles to the north), and cannot be solely relied upon to attract visitors. Instead, natural attributes must be considered within the pre-established framework based on infrastructure and management. Within these constraints, the landscape features described by Stuart-Street & Kirkpatrick (1994) and water bodies were assigned maximum points.

Threats and uses

Seven threats to the recreation use of sites were identified. These were assigned values from -5 (for a high threat) to 0 (no threat). Only four could be considered to be threats caused by recreation directly, dieback, vandalism, erosion and fire (possible increased incidence), although the latter also accounted for destruction of scenic amenity. The others (land claims, weed invasions and salinity) are primarily external threats. Land claims are not necessarily a threat to recreation, but its inclusion as a criterion recognises that liaison may need to be undertaken with Aboriginal interests prior to site development

The diversity of recreation opportunities was considered to be quite important in maximising visitor interest. The abundance of sites with singular features generally restricted the number of opportunities offered, hence sites featuring a range of opportunities were rewarded by the scoring system. The period of use and interpretive potential was similarly considered. Sites offering year-round use and interpretive opportunities were considered to be a more efficient use of development and management funds, and hence scored more points than seasonally-used sites, or those with limited interpretive opportunities.

Current and future management

Current management was considered an indicator of the commitment of LGAs to cater for recreation. Criteria included the general cleanliness of sites, and the level and quality of facilities provided. However, the other two criteria in this category (cost to establish infrastructure and the cost of serviceability/maintenance) contributed a possible 17% of the total score compared to 8.5% for current management. It was considered that the production of a regional framework for recreation/ tourism, and the identification of key sites, might provide the incentive for LGAs to establish sites and maintain them to the desired standard. The scores reflected this assumption.

Despite the systematic process used in assigning numeric values to criteria, the process has several inherent faults. Firstly, it could be argued that scores for each category are not representative of their relative importance. For example, natural attributes (within the physical attributes category) were assigned a maximum possible value of 50 out of a possible total score of 175. It could be argued that because natural attributes are the main attractions to visitors they should be rated higher. Conversely, threatening processes (*e.g.* fire) and problems with managing sites may lead to continuing degradation, despite high quality natural attributes. Further, it was accepted that LGAs could argue that the assigned values for each criterion might undervalue sites within their area. Discussions with seven shires following the assessment process indicated that this was not a problem within the Merredin District, but the assessment procedure should be able to accommodate such concerns when the situation arises.

Results

Sixty sites were assessed and ranked (Table 1). An analysis of the results revealed an abundance of sites with distinctive topographic features (typified by high scores for 'topographic complexity') or waterbodies (51% and 49% of sites respectively). A total of 78% of all sites featured one or both. This is indicative of the reserve selection system in the Wheatbelt, where almost all arable land was cleared and the reserve system based on the remaining non-productive sites. The bias toward waterbodies or distinctive topographic features was also evident in the results of the top 21 ranked sites; the top 21 ranked sites have been used for discussion purposes due to two sites being ranked equal 20th. Only five of the top 21 sites had neither (Kellerberrin–Trayning Road, Korrelocking Nature Reserve, Durokoppin Nature Reserve, Weira Reserve and Meckering Earthquake Fault).

The survey revealed only four sites where there were more than three possible recreation opportunities. All sites were ranked in the top 21 (Mt O'Brien, Mt Matilda NR, Karalee Rock and Sandford Rocks NR). Most sites offered nature study, picnicking or bushwalking on unmarked trails, whilst several lakes provided infrequent opportunities for water-skiing. There was also evidence of horse-riding, and possibly camping, at some sites. Water-skiing, horse-riding and camping are not permitted on nature reserves, but are allowed on LGA reserves at the discretion of the relevant authority.

The distribution of scores is illustrated in Fig 2. The graph shows a distinctive drop in the scores for those reserves ranked equal 15th (score=135) and those ranked equal 23rd (score=129). The location of the top 21 ranked sites is shown on Fig 3. The significance of the weighting for each criterion is demonstrated through the distribution of sites along major travel routes and near towns. Only Sandford Rocks and Billyacatting were further than 10 km from a recognised travel route, but scored highly in the other categories.

CALM is responsible for the management of seven of the top 21 sites; Mt Matilda NR, Baladjie Rock NR, Durokoppin NR, Bulgin Rock NR, Sandford Rock NR, Buntine NR and Korrelocking NR. The remainder are vested in LGAs, the Waters and Rivers Commission or the Water Corporation. The latter two are in the process of rationalising their reserve assets in the Merredin District, and offering those that no longer meet corporate requirements to CALM or LGAs.

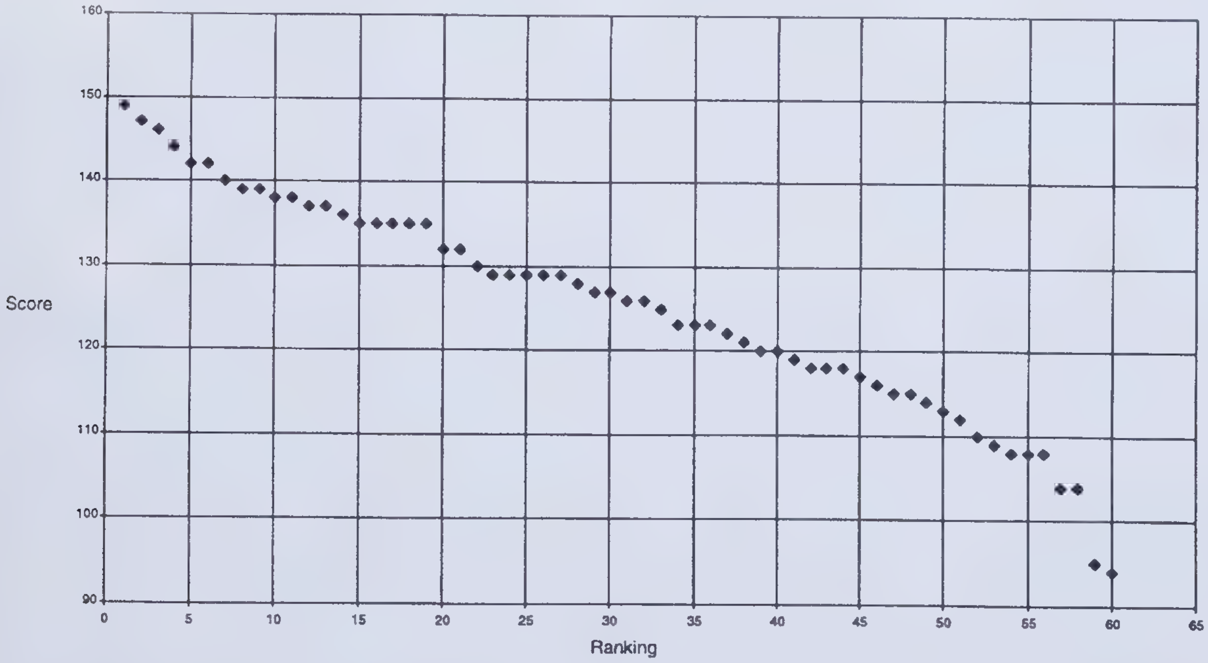
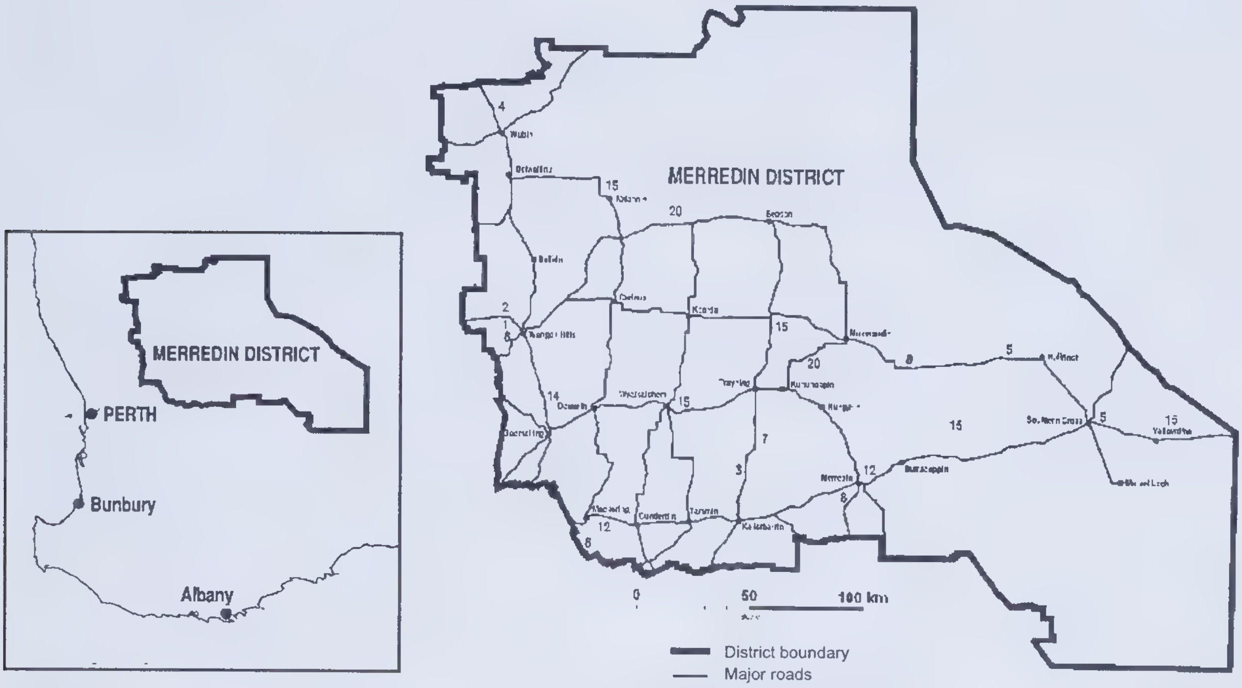


Figure 2. Distribution of scores for assessment and ranking of sixty reserves in the Merredin District (see Table 1).

Table 1.

Reserve rankings for the Merredin District

Rank	Reserve/Site	Shire	Physical Attributes (/100)	Threats and uses (/30)	Current and Future Management (/45)	Total (/175)
1	Mt O'Brien	Wongan–Ballidu	98	15	36	149
2	Mt Matilda Nature Reserve	Wongan–Ballidu	98	19	30	147
3	Kellerberrin–Trayning Road	Kellerberrin/Trayning	100	13	33	146
4	Buntine Rock Nature Reserve	Dalwallinu	93	11	40	144
5	Baladjie Lake Nature Reserve	Westonia	97	10	35	142
5	Hunts Soak	Yilgarn	95	12	35	142
7	Durokoppin Nature Reserve	Kellerberrin	95	11	34	140
8	Totagin	Merredin	95	7	37	139
8	Lake Ninan	Wongan–Ballidu	100	9	30	139
8	Weira Reserve	Mukinbudin	87	11	40	138
8	Meckering Earthquake Fault	Cunderdin	84	19	35	138
12	Merredin Peak	Merredin	95	7	35	137
12	Bulgin Rock Nature Reserve	Cunderdin	95	9	33	137
14	Oak Park Reserve	Goomalling	90	8	38	136
15	Xantippe Tank	Dalwallinu	93	9	33	135
15	Sandford Rocks Nature Reserve	Westonia	80	17	38	135
15	Korrelocking Nature Reserve	Wyalkatchem	91	8	35	135
15	Karalee Rock	Yilgarn	93	14	28	135
15	Mt Marshall	Mt Marshall	96	5	34	135
20	Mt Collier	Koorda	90	9	33	132
20	Billyacatting	Trayning	85	11	36	132
22	Culimbin Well	Dowerin	88	9	33	130
23	Kellerberrin Hill	Kellerberrin	88	6	35	129
23	Petrudor Rock	Dalwallinu	80	11	38	129
23	Eaglestone Rock/Lake Brown	Nungarin	83	10	36	129
23	Dingo Rock	Wongan–Ballidu	80	11	38	129
23	Namalcatching Nature Reserve	Dowerin	90	8	31	129
28	Burrocoppin Nature Reserve	Merredin	87	8	33	128
29	Mt Steven	Trayning	87	7	33	127
29	Cunderdin Hill	Cunderdin	86	6	35	127
31	Uberin Rock	Dowerin	80	12	34	126
31	Mt Stirling	Kellerberrin	80	10	36	126
33	Frog Rock Nature Reserve	Yilgarn	88	9	28	125
34	Reynoldsons Reserve	Wongan–Ballidu	86	3	34	123
34	Datjoin Well	Mt Marshall	75	11	37	123
34	Billiburning Rock	Mt Marshall	80	10	33	123
37	Pergandes	Mt Marshall	71	14	37	122
38	Danberrin Hill	Nungarin	78	9	35	121
39	Elachbutting Nature Reserve	Westonia	72	12	36	120
39	Charles Gardiner Nature Reserve	Tammin	80	8	32	120
41	De-erranning Reserve	Mukinbudin	78	8	33	119
42	Yorkrakine Rock Nature Reserve	Tammin	80	6	32	118
42	White Dam	Wyalkatchem	85	6	27	118
42	Mollerin Rock	Koorda	76	8	34	118
45	Waddouring Hill	Mt Marshall	77	7	33	117
46	Wubin Rock	Dalwallinu	77	4	35	116
47	Berringbooding Reserve	Mukinbudin	75	9	31	115
47	Chiddarcooping Nature Reserve	Westonia	73	9	33	115
49	Yannimooning	Westonia	73	9	32	114
50	'Sharks Mouth' (private property)	Kellerberrin	77	3	33	113
51	Gathercole	Wongan–Ballidu	75	3	34	112
52	Gnamma holes, Trayning–Bencubbin Road	Trayning	71	8	31	110
53	Lake MacDermott	Mt Marshall	70	7	32	109
54	Moningarin Tank	Koorda	71	5	32	108
54	Lake Campion (Ski Lake)	Nungarin	72	0	36	108
54	Wattonning Reserve	Mukinbudin	69	2	37	108
57	Trayning Well	Trayning	61	9	34	104
57	Baandee Lake	Kellerberrin	70	-2	36	104
57	Cailbro School Site	Dalwallinu	52	8	35	95
60	Newcalbeon	Koorda	56	5	33	94



Numbers correspond to rankings as per Table 1

Figure 3. Location of top 21 ranked recreational sites surveyed in the CALM Merridin District (see Table 1).

Discussion

It is clear from site inspections undertaken during the course of the project that almost all sites suffered from varying degrees of degradation due to recreation. Inappropriate siting, poor site design, and lack of active management, all contributed to negative impacts despite low visitor numbers. The most obvious impacts included;

- soil compaction and erosion of picnic sites and access tracks;
- loss of understorey species from picnic sites;
- extensive wanton destruction of exfoliated granite adjacent to visitor sites; and
- removal of timber for firewood.

Several sites were severely degraded, with Yorkrakine Rock probably the worst principally through loss of vegetation, erosion and graffiti. The main factors contributing to the level of degradation at this site were poor site design, the relatively high visitor numbers and long established use patterns. It is probable that many sites in the Wheatbelt will eventually suffer similar degradation unless recreational use of sites is rationalised, and those chosen are properly planned and managed (*e.g.* access to vandal prone sites is restricted, graffiti is removed immediately to discourage further efforts).

The arbitrary nature of the scoring system means that there is a possibility for disagreement over the rankings. Whilst the scoring system was ratified by the North Eastern Wheatbelt Travel (NEWTRAVEL) group of seven shires after brief examination, other shires may disagree. Safstrom (1995) detailed the various technical problems in assessing the conservation value of Wheatbelt reserves. He considered the applicability of scoring systems, iterative selection algorithms, irreplaceability, and multi-criteria analysis before deciding that the last method was most preferable. The main advantage of this method was the ability for different users to select appropriate criteria to suit their needs. The same principles can be applied to this study, enabling shires to agree on the most important criterion, or various combinations of criteria. This is readily achieved by filtering the data in an Excel spreadsheet to select the chosen criteria.

Although most of the discussion has concentrated on the top 21 sites, this is probably in excess of the number that should be considered for development at a District level. Given that the objectives of the strategy include reducing the amount of impacts to natural sites, development of any more would be self-defeating unless a large amount of management input could be ensured, which is unlikely. It is assumed, however, that not all of the top 21 sites would be developed. For example, LGAs may lack development funds, or the purpose of the reserve does not include recreation. Discussion of the top 21 reserves at least enables LGAs to be selective, and discuss options amongst themselves.

Conclusions

The results of the survey have acted as a guide to local authorities to identify and prioritise where efforts could be best directed within the Merredin District. CALM has an ongoing interest in the acceptance of the strategy, even when most of the reserves in the study area are managed by LGAs. As the primary conservation agency in WA, CALM has responsibility for the protection of wildlife on all lands, not just those managed by CALM. Further, some current recreation sites are located on CALM nature reserves that have been degraded due to resource constraints. To overcome these problems and to assist LGA development, CALM has collaborated with the LGAs in planning for future recreation and tourism use of high-ranking reserves. This has taken the form of informal partnerships where CALM has provided expert advice on site and facility design, and LGAs would maintain the sites. This is possibly a more efficient use of agency funds, rather than actively trying to manage the current number of widely dispersed sites. A corollary of the approach taken has been the use by LGAs of the rankings and CALM's site designs to apply for external grant funding. For example, the Shire of Wongan-Ballidu has obtained over $60 000 in grant funding to develop walking trails, interpretation and a lookout platform at Mt Matilda and Mt O'Brien. This success has led to CALM's Narrogin and Katanning Districts conducting similar ranking exercises within their operational areas, with a view to establishing collaborative recreation management with LGAs.

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Management of granite rocks

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Introduction

An earlier paper listed the uses to which granite rocks could be put (Main 1997). After noting that not all granite rocks were within reserves and that resources were not available to finance a physical presence by which management could be ensured, I concluded that rather than abandon granite rock islands to a management regime of benign neglect, an educated local public appreciative of the general values of granite rock islands could perhaps form a desirable starting point and a possible basis from which local groups could develop awareness and management programmes pertinent to their local situation and values.

In the above paper I tabulated the values of granite rock islands as perceived by various parties in the local and wider community. Broadly, values can be classified as economic, ecological or ethical. Using these headings one could regroup the headings used in the earlier paper as follows; economic, (utility), ecological (conservation), and ethical (recreation, heritage). This alternative classification not only serves to illustrate that classifications not only arrange information but in doing so colours and directs any debate which follows. Thus emphasising economic values suggests to those so oriented that obtaining the maximum benefit at least cost is a reasonable goal whereas emphasising utility lacks such an immediate connotation. In a similar manner, emphasising ecology may only carry a connotation of avoiding erosion or damage to vegetation, whereas conservation may imply denial of use or access. Likewise, recreational or historical values may be meaningless to some who on the other hand, may be receptive to the ethical concept of not denying future generations a resource enjoyed by the current one.

The foregoing serves to emphasise that all perceived values are not compatible. An appreciation of the diverse values placed on the same geographical features is a basis for the solution of any conflicts that will surely arise. Understanding and respect for the views of others is an integral component of compromise that is central to solving conflicts.

Formal methods can be devised to solve these potential conflicts and are based on community discussion leading to a wide-ranging awareness of all the values involved. The method involves assessing the likely outcomes of any of the alternative decisions that could be implemented; the likelihood that the decision will lead to the desired outcome; the regrets that follow from choosing one course of action than another and the regrets that might arise when the desired outcome is not forthcoming from the chosen action i.e. whether any salvage is possible. A judgement needs to be made of the acceptability or not of the likely losses arising from the alternative courses of action (Main 1992). The bottom line will be that there are some winners and some losers but importantly the public understands the process.

I need hardly draw attention to the fact that this ideal procedure has never been followed, especially with the uses to which granite rock islands are put. One of the reasons for this state of affairs is that in the past utilitarian values were pre-eminent. It is only recently that cultural, recreational, aesthetic and ethical values have achieved greater prominence. Thus, when decisions are being made now, there are likely to be expressions of interest in a greater diversity of values than was apparent in the past. Nevertheless it must not be assumed that past exploitation for utilitarian purposes completely destroyed the other values attributable to granite rock islands as illustrated by the following discussion.

Case Studies

Wave Rock, Hyden

Wave Rock, near Hyden, is an example of a site subject to a great variety of use without any assessment whatsoever, except of the utilitarian values of immediate interest. This example, as a case study, may help to develop a feeling for how past experience may be used to develop more general approaches to arriving at management decisions. Hyden is located in a very low rainfall area where potable water is at a premium. At the time it was decided to use the rock as a water catchment, the primary good was an economical and adequate supply of drinking quality water for the locality. Had a formal decision procedure been followed it could hardly have been expected to work; the area did not have a large population and what was there was interested in surviving rather than pursuing either cultural or ethical goals. Nevertheless, from the present vantage point it is possible to review what was lost by the development, the regrets; for example habitat formerly present beneath rock slabs when these were used to form the catchment directing rainfall into a holding area. A consequence of the redirected water flow was the reduction of water available to the vegetation of the area surrounding the rock. These costs are to be measured against gains that were principally a reliable water supply that could support a viable community. However, once the surrounding land was cleared the diversion of water probably helped reduce ground water recharge thus impinging on soil salinisation. What could not have been foreseen at the time of development and therefore unlikely to be included had a formal assessment been required was that once a local water supply was assured innovative local initiatives could develop the site as a locality attractive to tourists. It is only those of us who collected plants and animals in the early 1950's who have any measure of what has been lost or changed. For tourists and biologists visiting the area it is still regarded as being rich in the variety of plants and animals present.

A retrospective analysis by local citizens of the gains and losses over the period of development would undoubtedly yield insights into what the tangible and intangible costs and benefits have been. Such an analysis would be a great help to other local communities desiring to conserve or use local rock feature.

Other sites

In the early days of settlement granite rocks served as navigation aids for travellers. Later with the discovery of gold and the development of various fields such as Coolgardie and Kalgoorlie they marked the alignment of the various tracks by which access to the fields was obtained. The rocks also provided drinking water based on the supplies already developed by the Aborigines.

Among these access ways, the one from the west to the eastern goldfields and Holland's track from the south-west were much used. Some of the rocks have subsequently been developed for water supplies or used as picnic sites, for example Yorkrakine Rock north of Tammin, and Sanford Rock north of Westonia. Sanford Rock is a particularly interesting example of a site favoured by travellers because stock could be readily held in an area bounded by rocks. The site now provides an unstudied example of the way weedy species associated with stock and their grazing of native vegetation have affected the natural conservation values of the locality. Boyagin Rock, west of Brookton, is an example of a rock predominantly used as a picnic site.

Another use for water in gnammas occurred in the early years of land settlement following World War II when superphosphate bags were washed in them prior to being used for other purposes. Superficially these activities had little impact on the appearance of the rocks. However, the nutrient enrichment of the pools led to a massive increase in the abundance of filamentous algae. The changed ecology quickly led to the local extinction of a great variety of typical pond animals especially Crustacea. Whether these have re-invaded I do not know. Nor have I studied the effects of the overflow of nutrient enriched waters on the down-slope flora. Clearly the possibility of such events and possible anomalous distributions need to be taken into account when devising management plans designed to maintain distributions and diversity of the biota. The gnammas on Mount Grampthorne, east of Hyden, were conspicuous examples of such enrichment and changes in the biota during the 1960's. No doubt there are other examples.

Thus it would seem that past developments and uses have provided an array of granite rocks in agricultural, semi-arid and arid landscapes, some used for upwards of a century, which would now provide a rewarding comparative study of the way the rocks and their biota have responded. Such a study, if taken as an example of management by benign neglect, might reveal what needs to be undertaken in order to achieve minimal conservation management should it be needed for these important natural features.

A personal comment

As an outsider I have a bias in seeing granite rocks as a class of objects needing conservation attention; however, as already argued the central government is unlikely to participate because of the costs involved. I firmly believe that good management can arise from cooperative efforts of local people. Nevertheless I am acutely conscious of the other primary needs requiring attention, for example salinisation of the landscape as well as other problems broadly grouped as related to land care activities. These problems are compounded by withdrawal of quality community services formerly taken for granted, coupled with the ever present threat, in the current political environment, that the axe of economic rationalism will continue to be wielded leading to the further marginalisation of the countryside and its inhabitants.

Under these circumstances it is merely platitudinous to ask that locals, unassisted, take up the challenge of conserving granite rock islands and their associated values. In order to participate in conservation activities, locals need time and resources neither of which are in abundance in the present situation.

To an economic rationalist the foregoing arguments have little currency unless they can be seen as short term, income yielding actions, yet it is an International goal (IUCN/UNEP/WWF 1981) and State policy (Anon 1987) to retain biodiversity. The biota of granite rocks make a significant contribution to the States' biodiversity and clearly have a wide ranging attraction to a great variety of people (Nikulinsky & Hopper, 1999). It borders on irresponsibility to leave the care of these precious islands to already stretched locals; on the other hand it is not a viable option to impose a centralised command and control regime on them. In this sense education involves more than the local community which makes it more difficult because of the large numbers of potential participants in the decision. Yet if they have access to interesting and informative literature such as Nikulinsky & Hopper (1999) and Bayly (1999), then participants will inevitably bring a wider understanding to discussions and decisions. The value of granite rock islands is not solely in the biological components resident on them. Rock islands are a significant component of the landscape and an accessible interpretation of their significance in terms of recent history or the ancient river systems (now chains of salt lakes) and the way the present topography reflects the weathering and ancient erosion patterns of the river systems would contribute materially to the public's appreciation of the meaning of the landscape and the significance of granite rock islands as important watershed components of it (see Hocking & Cockbain 1990) and being determinants of the occurrence of many remnant and relict components of the biota.

This discussion suggests that management, even if acceptable goals could be set, involves much more than simple action or universally applicable recipes. No doubt many viable local solutions could be expected; however, as already discussed, the desire, will, time and resources are unlikely to be currently in abundance.

Conclusions

Discussions about management of public resources such as granite rocks should not be left to ' experts'; decisions should be transparent to be accepted by the public. For this to happen they must be involved. Thus their expertise should be acknowledged but in addition such activity will provide an opportunity for them to be better informed, (education without indoctrination).

If the public is to be involved in management it will require their devoting resources and time to the activity. Both are in short supply leading to the possible interpretation that leaving it to them is an abrogation of government function but local public issues are primarily the province of the public and should not be left to the expert. Hence the emphasis on transparency in decision-making. While I am conscious of the additional workload placed on citizens by this suggestion I am hopeful that it will be a focus should any discussions or local decisions on local granite rock islands be called for. Meanwhile until the issues raised and canvassed above are resolved, the question is whether a policy of benign neglect (do nothing) and its consequences are likely to be so regrettable that they are unacceptable? The history of the use made of Wave Rock, Hyden, along with its present acceptability as a destination for visitors suggests that there may yet be time for worthwhile values to remain while public awareness is heightened.

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ISLANDS IN THE BUSH: MANAGEMENT OF GRANITE OUTCROPS

WORKSHOP: Managing granite landscapes

Proposals for the protection and utilisation of granite hills

Following the presentation of papers concerned with various aspects of the natural history and utilisation of granite hills, with special reference to occurrences in the Wheatbelt of Western Australia, it became evident in discussion that the hills are regarded as resources on which there are conflicting, even mutually exclusive, claims. In particular, the granite exposures are variously of interest to those concerned with quarrying, water conservation, tourism, recreation, biological conservation and scientific research.

It was unanimously (or *nemine contradicente*?) agreed that rather than dealing with claims and proposals on an *ad hoc* basis (which offers no basis for comparative merits) these interests could best be served and evaluated by an overall review of the qualities of various exposures and a listing or register of all major occurrences and attributes together with a rating in terms of the various possible aspects and claims. It was agreed this register should be compiled by a group of independent, impartial and knowledgeable people.

To this end it was suggested that the Royal Society of Western Australia appoint a Working Party to initiate and oversee the project, and that funds be sought from government sources and private foundations. Such funds would be used first, for the appointment of an officer who would act as secretary and administrative coordinator for the project, and second, to underwrite the costs of the trial surveys and resultant reports and guide books, and any costs incurred by the Working Party in their technical role. The collaboration of a shire council, or councils, would be sought and welcomed, as would the involvement of interested local groups and residents.

It was suggested that various survey and assessment methods be trialled in small regions such as particular shires or regions (*e.g.* Kondinin and Dundas shires, and the Monadnock Conservation Park in the Darling Range, to test procedures and criteria in contrasted environments), and amending procedures in light of that experience. Principles, methods and criteria would be outlined and set out in a booklet or set of guide lines, so that they could be put into practice by multiple teams to produce a consistent state-wide review. The Society Working Party could help supervise the surveys in an effort to maintain consistency and resolve the problems and difficulties that would indubitably arise. Such surveys would not only form the basis for evaluation but would also produce a record of the granitic terrains at this time. Any assessment would be subject to consultation and review, but once finally determined should carry legal force.

Much of the basic information concerning the location, size and shape of granite outcrops in Western Australia is already published, for not only are most, and certainly all major, granite outcrops already delineated on geological survey maps but there is a complete coverage of air photographs, a considerable amount of topographic information is available, and detailed analysis of granite exposures from Landsat imagery is in train; all this in addition to special purpose maps, air photographs and reports. The problem is to collect, collate and coordinate the raw data and bring it together in a form suitable for use by survey and assessment groups.

In later discussion, several potential difficulties and concerns were aired. For example, the question of public liability on tourist sites, and of confidentiality in matters of Aboriginal sites were raised without being resolved. It was pointed out that the availability of a data-base on granite rocks may well invite unwelcome interest from developers for example, but ways of guarding against this and limiting access while following the principle of disseminating knowledge were not forthcoming. There was no unanimity as to what form of signage is most suitable in different situations and for different purposes, but it was agreed that protective measures must be in place before people were introduced to the sites. It was agreed that visitors should be gently but firmly directed along designated paths which lead to interesting but durable sites but away from delicate and vulnerable features. Any easily damaged sectors or features on or near designated paths should be protected, so that patches of soil and flora for example would be provided with paths or stepping stones of local rock or of suitable decking. The need to establish biological resource areas from which to restock depleted outcrops was recognised and unanimously supported.

Previous experience in Western Australia suggested that the support and goodwill of the geological fraternity (especially the mining and exploration or prospecting sectors) in the survey and assessment procedure would not be automatic and may not readily be obtained.

Thus, though some problems remain unresolved, they were raised and aired, and there was strong support for the establishment of an overall survey and evaluation of granite hills and unanimous agreement that the Royal Society ought to be the key player in organising and administering the survey.

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ISLANDS IN THE BUSH: MANAGEMENT OF GRANITE OUTCROPS

WORKSHOP: Fauna Reconstruction

The need for reconstruction

From the point of view of fauna, there is a need for reconstruction for most (if not all) granite outcrops, with the obvious taxa being

- mammals, which are sometimes conspicuous (*e.g.* rock wallabies) but usually aren't (*e.g.* small, nocturnal species);
- birds, none of which may be restricted to granite outcrops, but many species are conspicuous when present;
- reptiles, which may be common on granite outcrops and may be visible (*e.g.* the diurnal dragon lizard *Ctenophorus ornatus*) or nocturnal hence seldom seen (*e.g.* geckos);
- frogs, which may be easily heard as breeding choruses aroung granites, and observed as tadpoles in rock pools;
- invertebrates, an immense array of species ranging from relatively large and easily observed (*e.g.* large spiders) to minute and cryptic.

With respect to conserving species, it was discussed that the preference was to protect and nurture the species that are already present, and avoid translocation if at all possible. A primary need is to enhance existing populations and protect existing habitats. Translocation can disrupt genotypes, and have all sorts of biological implications and repercussions. For example, some translocated invertebrates could become pest species to other granite outcrop communities

A comment was that we need to look at the big picture. People (especially tourists) want to see cuddly furry animals. From the perspective of ecotourism, landscape management, and how we view the countryside, there is a need to see our native fauna back in the landscape. There was general discussion about this, and it was agreed that people also want to champion the invertebrate species as much as the native fauna.

If so, how do we do it?

There is an important role for the community in reconstruction of fauna – scientists are not likely to be the ones involved in the reconstruction although they may be an essential group. There is a need for scientists and government to work in partnership with local community groups.

There are a number of issues that need to be considered in fauna reconstruction;

- fauna survey booklet – a generally accessible booklet is required, to summarise survey procedures and provide information on identifying granite outcrop animals;
- education – it is especially important to change peoples attitudes towards the conservation value of invertebrates, by incorporation of invertebrates in signage (*i.e.* make invertebrates the "champion") and education of tour guides, including local guides;
- problems of small reserves – what granite rocks and of what minimum size, would you choose for fauna reconstruction, and what fauna groups are declining;
- long term baiting strategy for larger vertebrates – this is an extremely important issue for conserving the larger vertebrates; we need more baiting of other than CALM estate; baits need to be more accessible to farmers, *etc*, and baits need to be other than meat based.

What are the implications of successful restoration?

Short-term successful restoration of granite outcrops would have implications for long-term conservation of the restored environment and its environs.

- Adjacent landowners need to be able to control native predators and herbivores.
- Fox/cat control programs need to continue for a number of years (or indefinitely).
- Long-term restoration requires commitment from locals for restoration of granite rocks, and programs within local community involving local people
- Fox control is essential for restoration of ground-nesting birds – they are a "champion" for reconstruction as they
  - are vulnerable to predation,
  - need encouragement to breed up, and
  - stay within granite outcrops.

But, there is a danger of too many champions; they also need to be locally relevant to spark interest.

Translocations

Translocation is seen as an important tool for restoration of granite outcrops, but there are many complex issues related to the success or otherwise of translocation programs. There needs to be continuous monitoring, with follow-up; don't just translocate animals/plants and leave them. It is necessary to consider at physical conditions *e.g.* drought – don't translocate in drought season. It may be necessary to provide suitable corridors for birds as well as mammals. It is necessary to consider how quickly different types of animals recolonize restored areas, and what resources they need in adjacent areas either for feeding or breeding. We need to understand the role of natural predators, and how they may impact lesser known plants and invertebrate species. It is difficult to know what numbers you put into a given area, and the required balance of fauna and flora for long-term stability.

Fungi are an important and under-considered aspect of revegetation. There is a lack of fungi in many areas, having been destroyed by cultivation/paddocks, and often poor soils lack fungi *e.g.* woodlands around rocks. Macropods and woylies probably significantly impact fungi.

Fire and water are significant considerations for adjacent farmers. An antidote for poisons such as 1080 is needed, to enable fox control without killing domestic stock/dogs.

What are you managing for?

- Number of conflicting controls
- Recognise choices/objectives of granite outcrops
- Control weeds/fencing
- Long term commitment for management – resources, where do they come from, local communities, govt., what about in 10-20 years?
- Aboriginal heritage – be aware of the significance of some granite outcrops to the Aborigines

Invertebrate Restoration

Reconstructing invertebrate habitats on granite outcrops is an important aspect of granites restoration. Even small details might be very important, such as replacing loose rock flakes near pools, and if possible/practical replacing rocks back to bare granite slopes. Many invertebrates live under flat plates of rock *i.e.* require rock-on-rock not rock-on-soil. Lizards also need a scatter of slabs for shelter. Such physical restoration should recognise the need for diversity in the nature of rocks that are resplaced.

Ecotourism

It is important to recognise that restoration of granite outcrops involves economics, tourism and education. Ecotourism is one way of raising money for restoration projects. Tourists will pay to see the animals running about in restored granite outcrops and associated camping grounds, *etc.*

Education

Successful restoration of granite outcrops will be facilitated by educational involvement of all levels, from primary and high schools to universities. For example, Honours projects, and postgraduate projects, are a cost-effective a quick means for studying then planning and restoring granite ecosystems. There is a role of communities, especially at the primary and secondary school level, but also at the tertiary university level. Involvement of students in granite restoration projects can be facilitated immensely by local involvement, for example with free accommodation and travel.

Conclusion

Most granite outcrops have a current "purpose" and their role will be reviewed over the coming years from various viewpoints. It is hoped that CALM will ensure that rocks with conservation value will be managed by the necessary governing/local bodies, and that restoration and indefinite conservation can be managed by a combination of state and local government, involvement of the local inhabitants and land-owners, and students and scientists from local schools and state universities.

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Leschenault Inlet Special Issue

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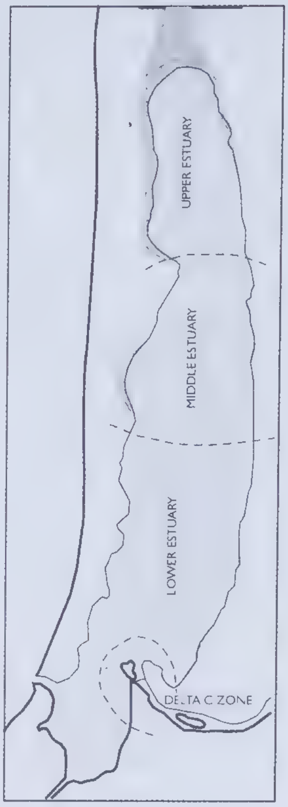
Preface: Leschenault Inlet Special Issue



Leschenault Inlet is an estuary located in the south-west of Western Australia, and is truly a special place. Over the past 20 years it has been studied by a number of researchers, and from their results it has become apparent that Leschenault Inlet is globally significant because of its biodiversity of microfauna, is nationally significant in terms of its geoheritage and mangroves, is of State-wide significance because of its peripheral vegetation, and is regionally significant because of its geomorphic setting and estuarine style.

The Royal Society of Western Australia has a long history in helping explore this state's biodiversity, and in publishing findings (the *Journal of the Royal Society of Western Australia* goes back to 1913, and through previous societies to 1897 as the *Journal of Proceedings of the Mueller Botanic Society of Western Australia*).

The Royal Society of Western Australia is publishing this Special Issue of its Journal to focus attention on the Leschenault Inlet estuary, bringing together a compendium of some 21 papers on the Inlet, detailing its physical environment, water quality, aquatic flora, fauna, avifauna, and management issues. This issue brings together for the first time a holistic and multi-disciplinary treatment of a linked coastal-marine environment in Western Australia, to a level not before achieved.

Following publication of the Special Issue, a weekend symposium workshop on the Leschenault Inlet environment will be held at Bunbury and Leschenault Inlet, in October 2001. This symposium workshop will bring together researchers, university personnel and students, community and conservation groups, and government personnel in a combined conference and excursion. This special issue provides a framework for fruitful synergistic discussions and hopefully actions at the symposium workshop and excursion.

This Special Issue on Leschenault Inlet is large, some 300 pages, and exceeds the normal annual journal length of the Royal Society, and hence required case binding. It was dedicated as the December issue for the year 2000 so that it would fit at the end of the normally library bound run.

A number of individuals contributed editorially and administratively to the publication this Special Issue, spending long hours editing and proofing manuscripts, and drafting diagrams for the various papers herein. Thanks are extended to P Clifford, J Unno, M Brocx, T Nisbet, and C Miskell for their editorial assistance and contributions to the drafting of the cover.

This Special Issue would not have been possible without funding external to the Royal Society, and here we would like to extend our appreciation to the following organisations that generously contributed funds: the Gordon Reid Foundation for Conservation, the Marine, Coasts and Wetlands Branch of Environment Australia, and VCSRG.

Dr Vic Semeniuk & Dr Philip Withers

Editors, The Leschenault Inlet Special Issue

Western Australia

Environment Australia

WATER AND RIVERS COMMISSION
LESCHENAULT INLET MANAGEMENT AUTHORITY

VCSRG

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The Leschenault Inlet estuary: an overview

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Abstract

The Leschenault Inlet estuary is an elongate shore-parallel, shallow water estuarine lagoon with distinctive patterns of bathymetry and geomorphology, framed to the east by the Mandurah-Eaton Ridge, to the west by a dune barrier, and to the south by two deltas. The estuary is diurnally micro-tidal, wave dominated and wind current driven. Estuarine waters are close to marine salinity but annually poikilosaline. Four salinity fields are recognised, corresponding to the delta zone, the lower estuary, the mid estuary, and the upper estuary. Large scale stratigraphic relationships within the system are relatively simple, with estuarine sediments to the east onlapping a quartz sand ridge, and a dune barrier encroaching over estuarine sediments to the west. Sedimentary patterns are underpinned by geomorphology, linked to the nature of shorelines, reworking sources and hydrodynamics, with muddy sediments accumulating in deeper water basins and semi-sheltered environments, and sand accumulating on exposed platforms, dune margins, or in deltas. The dune barrier, underlain by fresh water, separates oceanic and estuarine waters, with a saline/freshwater interface on both sides. Freshwater discharges from the barrier form shore seepages, which are important for shore vegetation and faunal use.

Leschenault Inlet estuary is unique in south-western Australia for several reasons. Formed behind a shore-parallel dune barrier, and wholly Holocene in age, its estuarine geomorphology and hydrologic structure are different to other local estuaries such as the Swan River Estuary and the Peel-Harvey Estuary. The estuary does not represent a simple river-to-sea transition, but has rivers entering at one end of a long coastal lagoon formed by marine processes rather than fluvial erosion. Leschenault Inlet estuary also has had a complicated Holocene sea level history, resulting in complexity of its shores. The western shore is further complicated as parabolic dunes encroach into the estuary, producing a varied assemblage of shore types and stratigraphic/hydrologic situations. The complex of shores and wetland types peripheral to the estuary support five types of fringing vegetation. Consequently, Leschenault Inlet estuary is a classic area for studies of ecology of estuarine peripheral vegetation, and the system ranks as one of the most significant in southern and south-western Australia. Through its proximity to the Leeuwin Current, the estuary also supports the most southern occurrence in Western Australia of the mangrove *Avicennia marina*, and the array of landforms and vegetation in and around the estuary combine to create an important classroom for palynology.

With numerous low-tidal to subtidal benthic habitats in the estuary, there is a rich diversity of flora and fauna: 3 species of seagrass, 7 species of algae, 31 species of mollusc (6 common species), 21 species of small benthic crustaceans, several species of larger crustaceans including the Blue swimmer crab (*Portunus pelagicus*), 15 polychaete species, and a normally oceanic ophiuroid echinoderm. The foraminifera assemblages in the estuary also are unusually diverse. Forty two species of fish have been recorded from nearshore and shallow waters. The estuary also is important for waterbirds, and as a dry season refuge in mid spring and summer it ranks amongst the top wetlands in south-western Australia.

Land reclamation, dredging, harbour reconstruction and urbanisation have impacted the estuary in the past 60 years. The estuary currently also is mildly enriched in nutrients introduced during winter freshwater influx. Studies on the phosphorous content of mud, phytoplankton and aquatic macrophytes of the estuary, however, suggest that the impact of nutrients on the estuary to date has been small. The long-term effects of development impacts on the unique characteristics of the estuary, however, are currently unknown.

Keywords: Leschenault Inlet, estuary, sediments, vegetation, fauna, ecology, south-western Australia.

Introduction

Leschenault Inlet estuary is a shallow estuarine lagoon located along the coast in the southern part of the Swan Coastal Plain (Semeniuk & Meagher 1981a), in the Leschenault-Preston Sector of Searle & Semeniuk (1985). It is set in a subtropical subhumid climate, or Mediterranean climate (Gentilli 1972). It is the estuary of the Collie-Brunswick rivers and the Preston-Ferguson rivers (Fig 1). The estuarine lagoon is separated from the Indian Ocean and Rottnest Shelf by a barrier dune system, the Leschenault Peninsula (Semeniuk 1985).

This paper provides an overview of the Leschenault Inlet estuarine lagoon from several perspectives, mostly drawing from contributions in this Special Issue. Firstly,

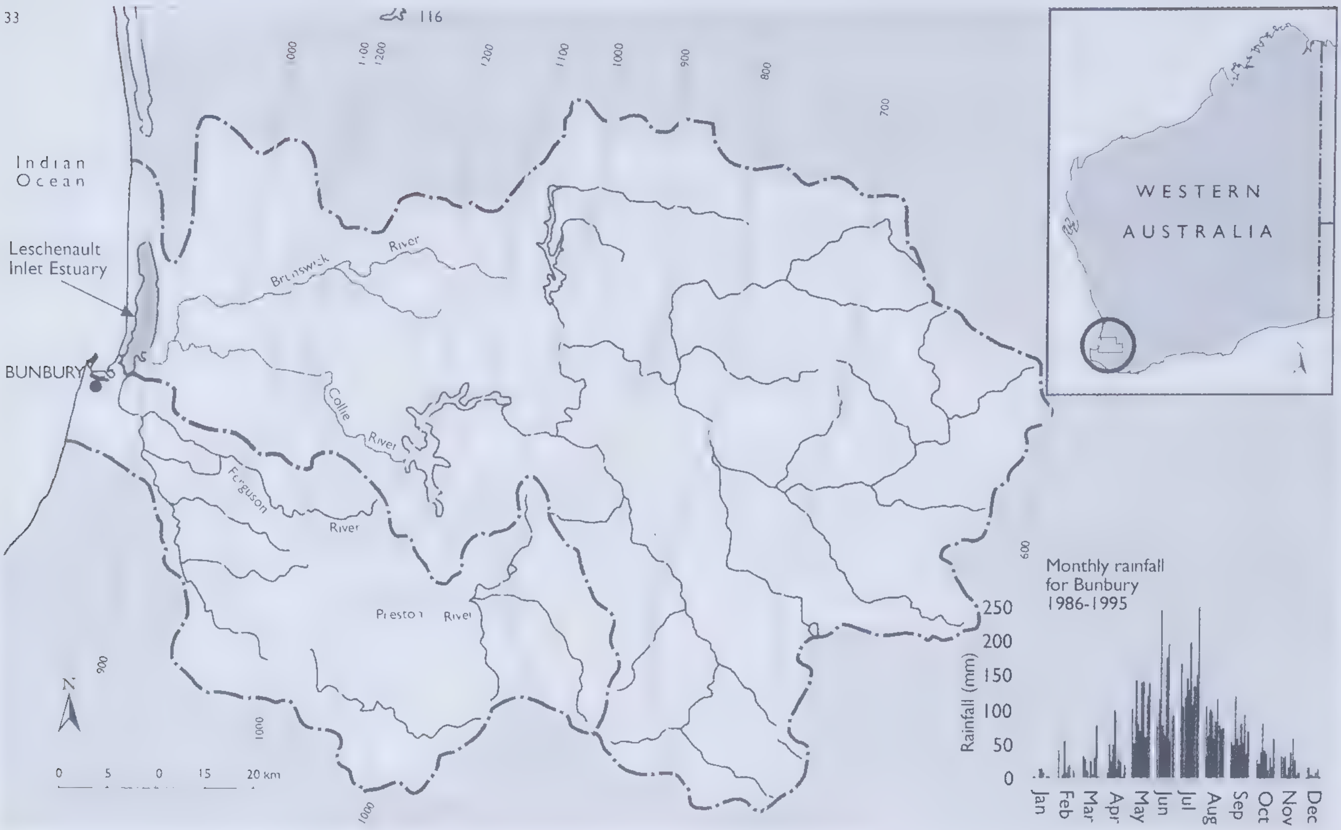

Figure 1. Location of Leschenault Inlet estuary showing setting within the extensive drainage basin of the Collie, Brunswick, Preston and Ferguson rivers, and rainfall isohyets in millimeters (data source Anon 1996). Rainfall graph for Bunbury shows monthly rainfall for 10 years (within each month, the vertical bars record monthly rainfall from left to right for each year from 1986 to 1995; data source Bureau of Meteorology, Perth)

its definition, geohistorical context and origin are described. A synthesis of its environmental aspects in terms of geomorphology, peripheral hydrology, water quality, estuarine hydrodynamics, sediments and habitats follows. Summaries of its biotic characteristics are presented *viz* its invertebrate fauna, fish, avifauna, and the population dynamics of selected groups, as well as subaquatic and peripheral vegetation. The paper concludes with a description of the range of human impacts on the estuary.

While the range of papers noted above deal with abiotic, biotic and ecologic aspects of the estuarine environment, small-scale and microscale habitats and their biota to date have not been considered in detail. These include the small-scale habitats contrasts of megaripples and sand waves and their intervening troughs, and microhabitats of *in situ* tree trunks, transported logs and other wood as benthic substrates, rock pebbles derived from locally eroding calcrete cliffs on the western shore or from eroded ferricrete on the eastern shore, isolated shells and shell pavements, cohesive mud cliffs along the saltmarsh shore, and limestone pavements. Such microhabitats provide the only localised hard substrate in the estuary; supporting localised populations of algae, diatoms, crustaceans, polychaetes, serpulid worms, ascidians, barnacles, mussels, bryozoa, and small rock crabs.

Leschenault Inlet estuary

Leschenault Inlet estuary encompasses an estuarine lagoon barred by a Holocene dune barrier. Some authors refer to the estuary simply as "Leschenault Inlet", or more recently, as "Leschenault Estuary". The term "Leschenault Inlet" once referred to the entire narrow water body comprising a barred estuarine lagoon and a river channel connecting it to the ocean (Fig 2). By definition, an inlet is "a short narrow waterway between islands, or connecting a bay, lagoon, or similar body of water with a larger body of water, such as a sea or lake" (Bates & Jackson 1997). The term "inlet" is not synonymous with "estuary".

Strictly, the name "Leschenault Inlet" should have been applied only to the narrow opening connecting the lagoon with the Ocean, and "Leschenault Lagoon" should have been applied to the larger water body, but the name "Leschenault Inlet" was applied to the lagoonal water body and to its narrow (tidal and fluvial) connection to the sea. Engineering modifications in southern parts of the former Leschenault Inlet severed the system into two. The Department of Marine & Harbours, the Leschenault Inlet Management Authority, and the Department of Land Administration then renamed the system: the original narrow connection was called "Leschenault Inlet", and the larger water body "Leschenault Estuary".

The definition of an estuary has been long debated in the literature, and has significantly progressed from its original hydrochemical concept, *viz* "a body of water where

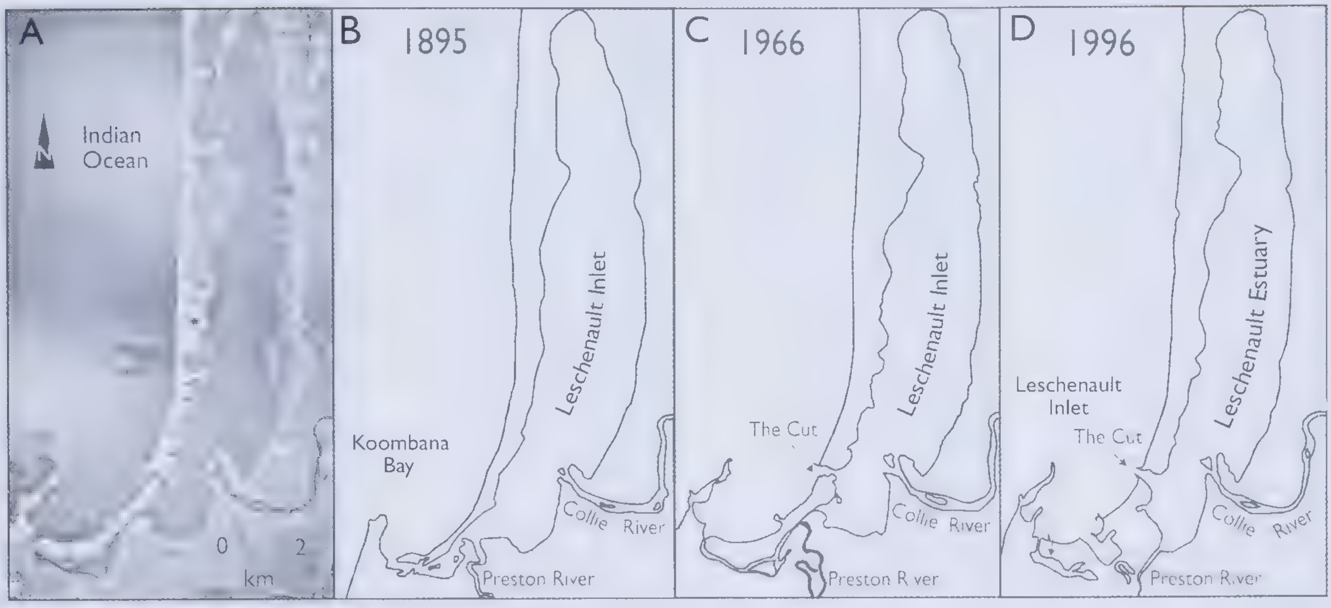

Figure 2. A: Aerial photograph of Leschenault Inlet estuary showing barrier dune separating the elongate lagoon from the Indian Ocean, and the Collie River delta to the southeast. **B:** Map of Leschenault Inlet in 1895 showing continuous waterway from the ocean inlet to the south to the elongate landlocked estuarine lagoon. **C:** Map of Leschenault Inlet in 1996 showing first impact on the system by an artificial breach in the dune barrier referred to as "The Cut". **D:** Map showing terrain modification severing Leschenault Inlet, and terminology of the Leschenault Inlet area during the 1980s and 1990s.

river water mixes with and measurably dilutes sea water" (Ketchum 1951). Perillo (1995) distilled 40 dictionaries, encyclopedia and specialist references to define an estuary as "a semi-enclosed coastal body of water that extends to the effective limit of tidal influence, within which sea water entering from one or more free connections with the open sea, or any other saline coastal body of water, is significantly diluted with fresh water derived from land drainage, and can sustain euryhaline biological species for either part or the whole of their life cycle." This definition, the most comprehensive to date, encompassing geomorphic, hydrodynamic, hydrochemical and biological aspects of estuaries, expands on the long accepted definition of Pritchard (1967), and addresses the difficulties raised by Day (1981). The system devised by Digby *et al.* (1999), a national classification proposed for Australian estuaries, which through application captures coastal embayments such as Shark Bay and partly land-locked ocean-connected waterways such as Port Hedland Harbour as estuaries, is conceptually flawed and is not used here. That used by Dalrymple *et al.* (1992), an internationally proposed classification of estuaries based on wholly sedimentologic criteria essentially is a classification founded on what is considered to be useful geologically or palaeoenvironmentally, and also is not used here.

Leschenault Inlet estuary accords with the definition of Perillo (1995). It is a semi-enclosed lagoon, with the Preston and Collie Rivers contributing freshwater and fluvial sediments, with marine water exchanges and tidal influences propagated through a narrow, artificial opening ("The Cut") in the dune barrier, and where euryhaline fauna are sustained for all or part of their life cycle. The full extent of the estuary encompasses the large lagoonal water body and the lower reaches of the Collie River to the limit of the tides and brackish water (Fig 3). The limit of the estuary into the lower reaches of the Preston River diversion channel is sharply delimited by engineering modifications and landfill.

Against this background, we term the large water body "Leschenault Inlet estuary", rather than "Leschenault Estuary", for several reasons. The name "Leschenault Inlet" has precedence, and the larger part of the water body should retain the original name. Moreover, since the larger water body is still estuarine (receiving freshwater from the Collie and Preston Rivers, albeit the latter discharges into the larger water body through a diversion channel), the term "Leschenault Inlet estuary" is apt. Ideally, the term "estuary" should be applied to the river-to-ocean transition, however, "Leschenault Inlet" is too entrenched as a name to supplant it with "the Collie-Preston River estuary". In technical terms, the system now is comprised of the Collie River Estuary, the Preston River Estuary, and the Leschenault Inlet estuarine lagoon. The smaller part of the severed water body, once the original oceanic opening to Leschenault Inlet and the outlet of the Preston River, and now essentially a tide-influenced marine inlet, is no longer estuarine. Here we retain the name "Leschenault Inlet".

The estuary earlier in the Holocene

The Leschenault Inlet estuary has had a history influenced by a retreating barrier, and a fluctuating sea level. Earlier in the Holocene, between 7 000 years and *ca* 2 500 years BP, the estuarine lagoon was longer and wider, as indicated by stratigraphic studies, radiometric dates and the erosional history along the Leschenault-Preston Barrier (Semeniuk & Meagher 1981a,b; Semeniuk & Searle 1986, 1987; Semeniuk 1985, 1995a,b). The original proto-estuarine lagoon originated 7 000 years BP, with the construction of a shore-parallel barrier dune. At that stage, the estuary extended as far as northern Lake Preston, and was at least three times as wide. Fossil molluscs and sediments indicate that estuarine conditions existed along

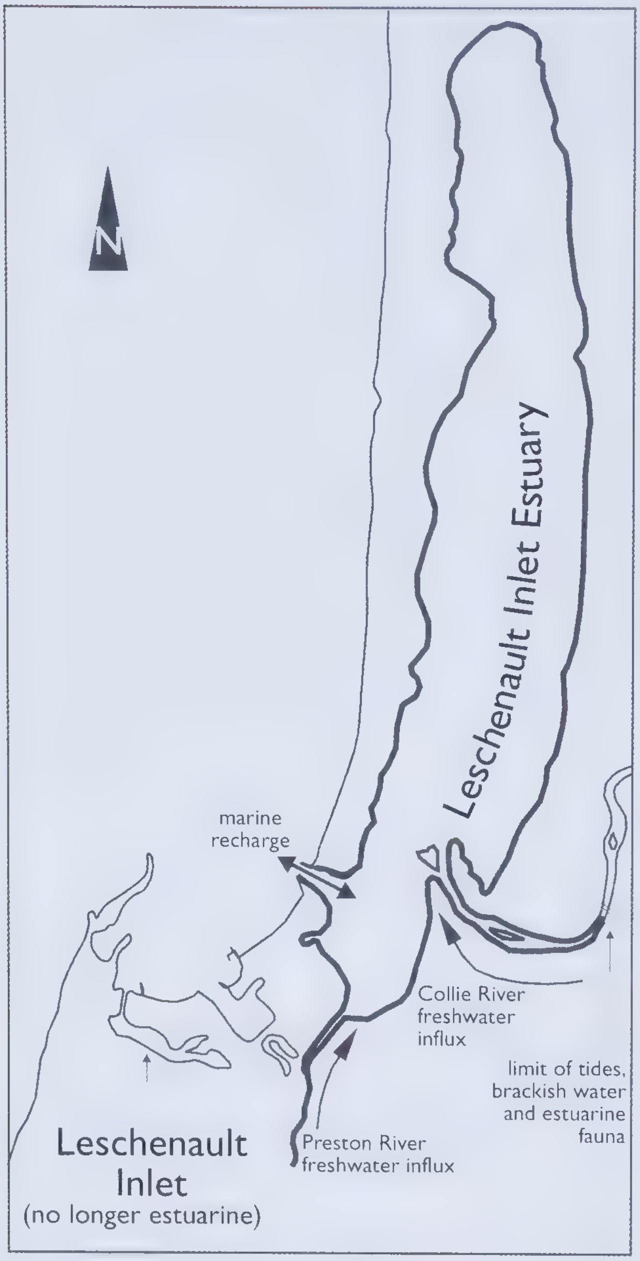
N
Leschenault Inlet Estuary
marine recharge
Collie River freshwater influx
limit of tides, brackish water and estuarine fauna
Preston River freshwater influx
Leschenault Inlet
(no longer estuarine)

Figure 3. Terminology for the Leschenault Inlet estuary used in this paper, and extent of the Leschenault Inlet estuary.

the entire length of the lagoon, which resembled a system like The Coorong in South Australia.

With the eastward advance of parabolic dunes and the retreat of the barrier (Semeniuk 1985), the estuarine lagoon progressively became narrower, until a series of parabolic dunes *ca* 4 500 years BP crossed its narrowest part opposite a coastal limestone projection (a Pleistocene cuspate foreland; Semeniuk 1997) segmenting the proto-estuarine lagoon into a northern part (Lake Preston, now uninfluenced by river input, and hence no longer estuarine), and a southern part (the present estuary influenced by the Preston and Collie rivers). Sea level rising to 3-4 m above present *ca* 4 500 years BP flooded the lowlands marginal to the estuary, increasing its width. With falling sea level, the lagoon marginally became narrower. Ongoing parabolic dune encroachment has progressively narrowed the estuarine lagoon. The shape, length, and extent of the estuary during various stages of the Holocene is shown in Fig 4.

Estuarine geomorphology

The main landform and estuarine units that border and constitute the Leschenault Inlet estuary are (Fig 5):

- to the east, the Mandurah-Eaton Ridge, a moderately high ridge of Pleistocene quartz sand and limestone, and lowlands underlain by Pleistocene limestone referred to the Yalgorup Plain (Semeniuk 1995a, 1997);
- Leschenault Inlet estuary itself *i.e.* the elongate shore-parallel, shallow water estuarine lagoon;
- two deltas, the Collie River Delta and the Preston River Delta, that enter the estuarine lagoon from the south-east and south; and
- to the west, the Leschenault Peninsula, a moderately high quartz and carbonate sand Holocene dune barrier (Semeniuk 1985).

Based on its geomorphic setting, hydrodynamics, and morphology, the estuary can be classed as a microtidal barrier lagoon estuary (*cf* Hayes 1975). Hesp (1984) classes it as a barrier estuary, *i.e.* one that occupies an inter-barrier depression, and Perillo (1995) and Isla (1995) would class it as a "coastal lagoon" estuary.

The Leschenault Inlet estuary has distinctive patterns of bathymetry and geomorphology (Fig 5). The subtidal part is a flat-floored, elongate central basin, generally 1.2-2.0 m deep, flanked to east and west by shallow, shore-parallel platforms and ramps sloping from intertidal to 1 m depths. To the south, the central basin adjoins deltas, and to the north it grades into a shallow water flat, which further grades to extensive tidal and supratidal flats. High tidal to supratidal zones (saltmarsh flats) are developed along the eastern shore, in the middle to northern parts of the western shore, and to the north. Spits, and bar-and-lagoon complexes are developed locally along the southern to middle part of the western shore.

The stratigraphic framework is summarised in Fig 6. Estuarine mud, muddy sand and sand referred to the Leschenault Formation is Holocene in age, and < 7 000 yrs in age. This formation onlaps the Pleistocene ridge of sand (the Eaton Sand) and limestone to the east, overlies Pleistocene limestone (the Kooallup Limestone) at depth in the central and western parts of the system, and is itself overlain by a shoestring eastward retrograding body of Holocene dune sand (the Safety Bay Sand) to the west.

Salinity and hydrochemistry

Waters in the estuary are annually poikilosaline. In winter, the salinity generally decreases with the influx of fresh water from rivers, drains, run-off, and groundwater seepage (*e.g.* from dunes and deltas). In summer, evaporation (induced by increased temperatures and wind) and the continued exchange with the ocean influence the salinity, such that to the north, estuarine waters are often hypersaline. Wurm & Semeniuk (2000) divide the estuary into 4 salinity fields based on mean salinity and its variation throughout the year (Fig 7):

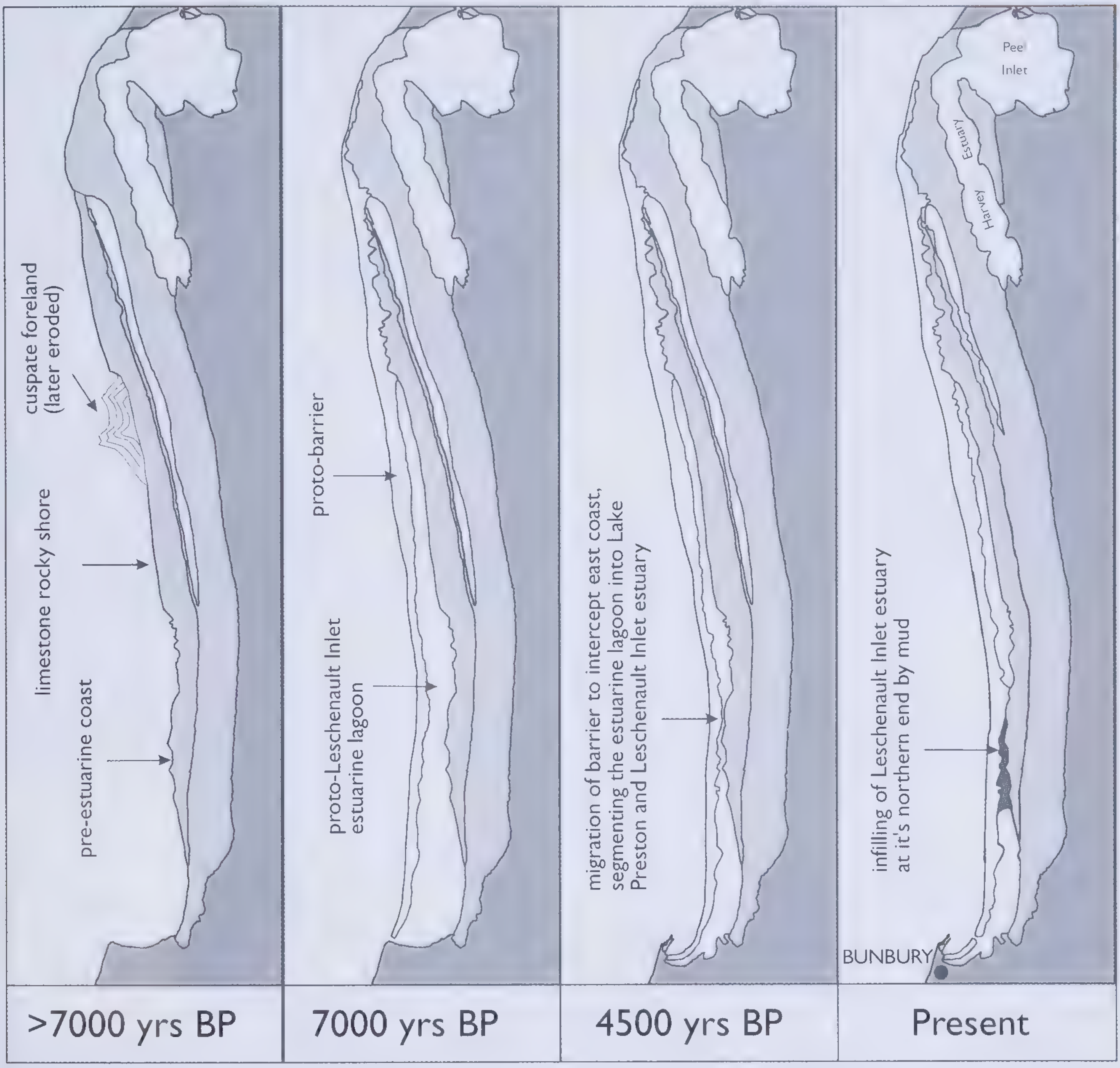

Figure 4. Evolution of the Leschenault Inlet estuarine lagoon during various stages of the Holocene. Before 7 000 yrs BP, the coast between Mandurah and Bunbury was an open limestone rocky shore, with a discrete cuspate foreland to the north. A dune barrier developed about 7 000 yrs BP forming a long barred estuarine lagoon that encompassed the present Leschenault Inlet system and Lake Preston. At *c* 4 500 yrs BP, the dune barrier impinged onto the eastern estuary shore segmenting the estuarine lagoon. The estuarine lagoon began to infill with mud in its northern portion.

- a deltaic field, where mean salinity influenced by river freshwater is slightly less than seawater but with a large variability about the mean (*e.g.* Collie River Delta area);
- a lower estuarine field, in which mean salinity is slightly greater than sea water, with a small variability about the mean within a mesosaline regime;
- a mid estuarine field, in which mean salinity is higher than sea water, with a large variability about the mean within a mesosaline regime; and
- an upper estuarine field, in which mean salinity is much greater than sea water, with a very large annual variability about the mean from hyposaline to hypersaline.

The classification of salinity used by Wurm & Semeniuk (2000) follows Hammer (1986), which encompasses salinities from fresh to hypersaline. Other workers at times use the Venice system (Anon 1959) to classify salinity of the brackish water spectrum of estuarine waters. A comparison between these classifications is shown in Table 1.

Table 1. Comparison of salinity between Hammer (1986) and the Venice System

Hammer	Salinity	Venice	Salinity
Fresh	< 0.5 ‰	Fresh	< 0.5 ‰
Subsaline	0.5-3 ‰	Oligohaline	0.5-5 ‰
Hyposaline	3-20 ‰	Mesohaline	5-18 ‰
Mesosaline	20-50 ‰	Polyhaline	18-30 ‰
		Euhaline	30-40 ‰
Hypersaline	> 50 ‰		

Salinity structure of the Leschenault Inlet estuary is complex as a result of the interplay of daily marine recharge through "The Cut", summer hypersalinity in northern parts of the lagoon, freshwater seepages from the adjoining uplands, and winter freshwater flooding from the Collie River. The estuary generally has no vertical stratification in salinity, but there is a south to north salinity gradient for most seasons. Short term and weak stratification exists during times of freshwater influx, and when there are water bodies of contrasting salinities, induced either by tidal recharge, or slugs of freshwater from the Collie River (Fig 7). Within the context of the elongate estuarine lagoon, overall, the estuary is well mixed in summer, and a positive estuary in winter along both the south to north lagoon transition, and the east to west Collie River to "The Cut" transition. The salinity dynamics along the east to west gradient from the middle reaches of the Collie River to "The Cut" have yet to be fully explored.

Water temperatures of the estuary are largely determined by air temperature and wind. Shallow water on the platforms, Collie delta and the northern flat have winter temperatures of *ca* 15 °C, and summer temperatures of *ca* 30 °C, with annual temperature fluctuations of *ca* 14 °C. Deeper water of the central basin has winter temperatures frequently below 15°C and summer temperatures at or

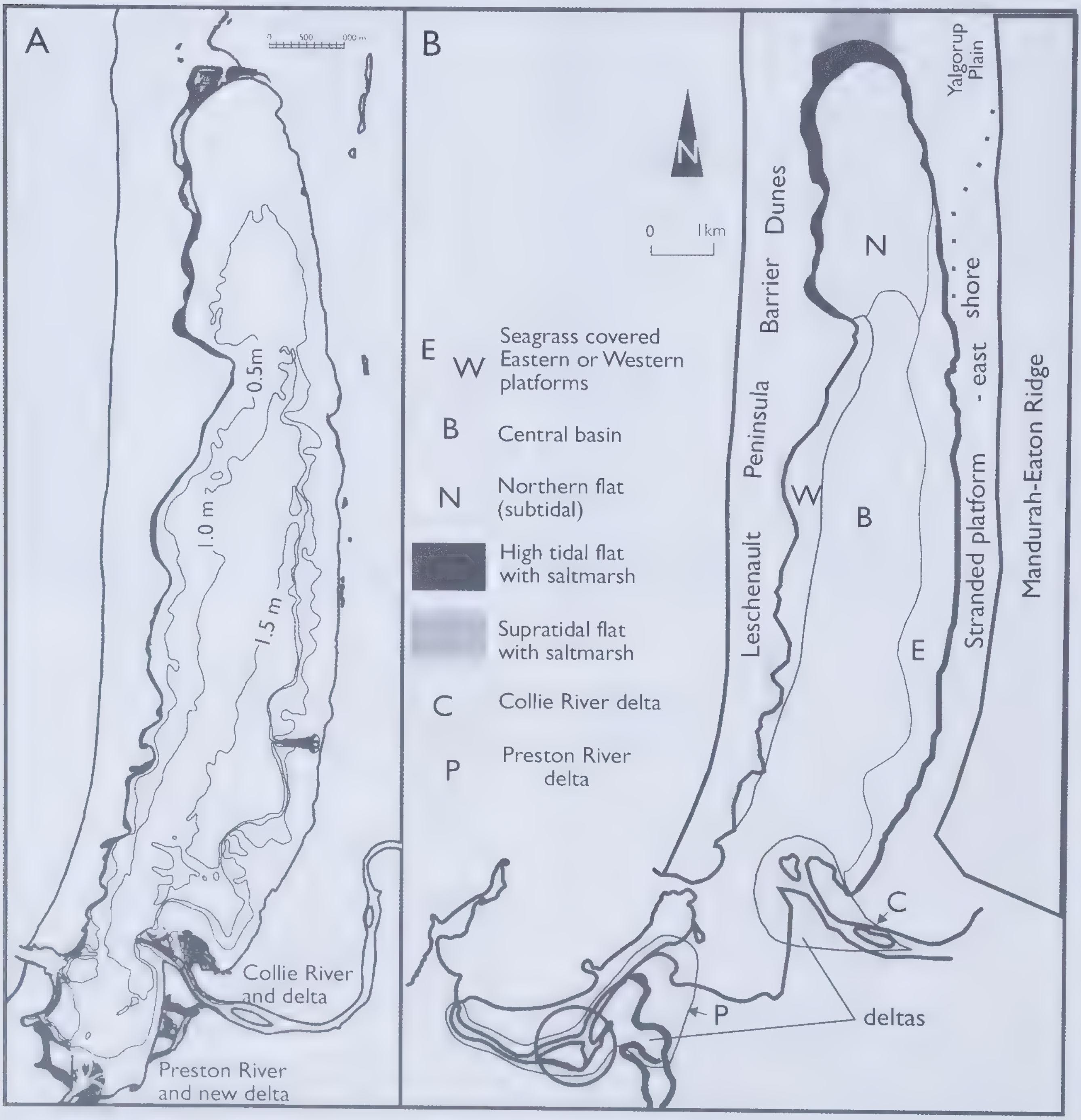
A
0 500 000 m
0.5m
1.0 m
1.5 m
Collie River and delta
Preston River and new delta
B
N
0 1km
E W Seagrass covered Eastern or Western platforms
B Central basin
N Northern flat (subtidal)
High tidal flat with saltmarsh
Supratidal flat with saltmarsh
C Collie River delta
P Preston River delta
Leschenault Peninsula Barrier Dunes
Yalgorup Plain
Stranded platform - east shore
Mandurah-Eaton Ridge
N
W
B
E
C
P
deltas

Figure 5. A: Bathymetry of the estuarine lagoon. **B:** Geomorphic units framing the estuarine lagoon, and geomorphic unit within the estuarine lagoon.

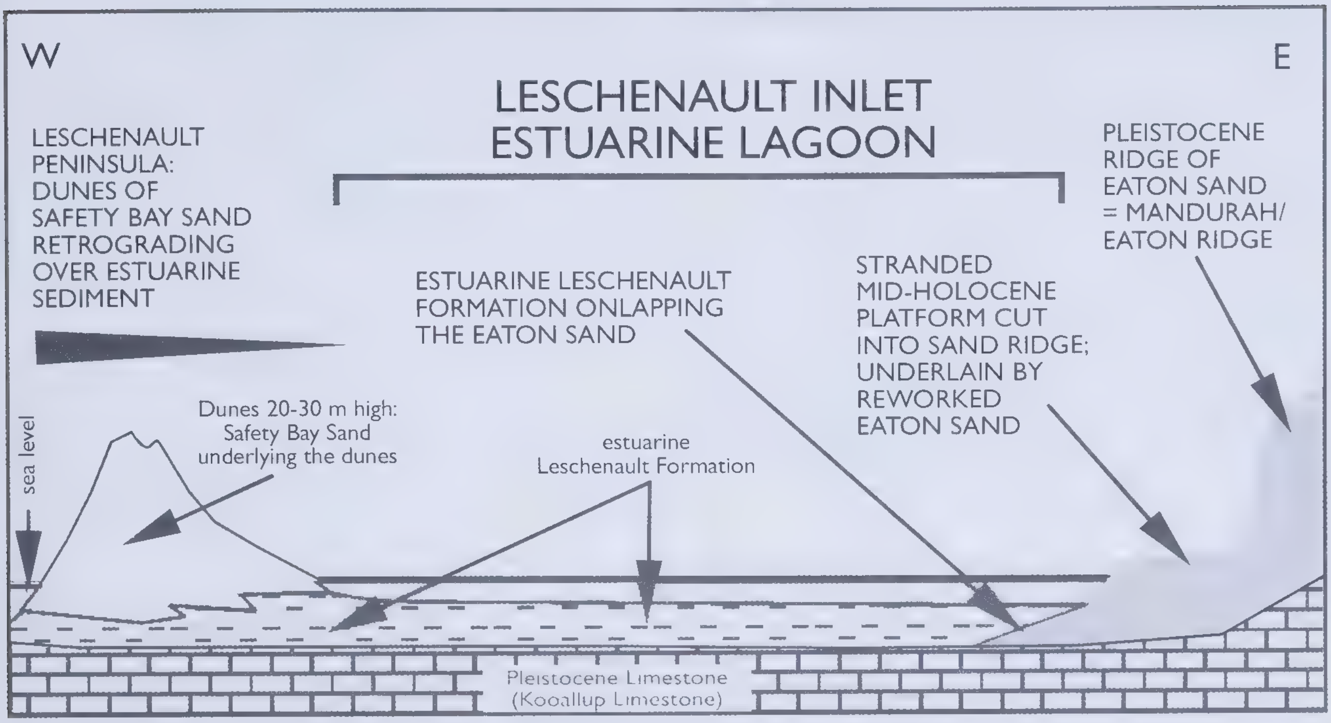
W
E
LESCHENAULT INLET ESTUARINE LAGOON
LESCHENAULT PENINSULA: DUNES OF SAFETY BAY SAND RETROGRADING OVER ESTUARINE SEDIMENT
ESTUARINE LESCHENAULT FORMATION ONLAPPING THE EATON SAND
STRANDED MID-HOLOCENE PLATFORM CUT INTO SAND RIDGE; UNDERLAIN BY REWORKED EATON SAND
PLEISTOCENE RIDGE OF EATON SAND = MANDURAH/ EATON RIDGE
sea level
Dunes 20-30 m high: Safety Bay Sand underlying the dunes
estuarine Leschenault Formation
Pleistocene Limestone (Kooallup Limestone)

Figure 6. Stratigraphic framework of the Leschenault Inlet estuary (information from Semeniuk 1985, 1995a).

above 25 °C, with annual temperature fluctuations of *ca* 10 °C. The estuarine waters are well oxygenated throughout the year with dissolved oxygen concentrations, even in summer, generally > 5 mg L^{-1}. The highest oxygen values occur at shallow water vegetated sites.

Hydrodynamics

The estuary is wave dominated and wind current driven. Summer seabreezes and landbreezes generate short period waves. Winter storms deriving from the northwest generate larger period waves. Periodically, cyclones in the region, through low pressure and storm surge elevate water levels up to 2 m (*cf* Cyclone Alby in 1978; Semeniuk & Meagher 1981a,b). Tides are diurnal, micro-tidal, with a mean spring range of 0.5 m. Atmospheric pressure influences water level more than astronomical tides, with high pressure in summer contributing to low tides, and low pressure in winter resulting in a small general rise in mean sea level (Semeniuk & Meagher 1981a). Tidal exchange and wind shear generate currents, generally aligned south to north, with a net drift northwards, transporting suspended mud and algae and sea-wrack to northern parts of the system. More complicated patterns occur in the southern estuary because of interacting ocean exchanges, river flow, wind induced currents, and complex bathymetry and shorelines of deltas and prominences. As is typical of estuaries, Leschenault Inlet estuary commonly is turbid due to mud re-suspended by wave action.

Modeling the circulation under a variety of tidal, river flow and wind conditions *e.g.* typical summer or winter ebb and flood tide, and a typical summer with a sea breeze coinciding with flood tide (Charteris & Deeley 2000) shows significant attenuation of the ocean tidal range in the estuary, a 4 to 7 hour phase lag for high and low water between the ocean and estuary (due to hydraulic restriction by "The Cut"), and a similarity of circulation patterns for summer and winter conditions. Mean water level in the estuary also appears influenced by river flow and generally is high during winter when river flows are highest.

Sedimentology

At the largest scale, sedimentary patterns and Holocene stratigraphic relationships within the estuary are relatively simple (Fig 6). A shore-parallel wedge of sand reworked from eastern shore Pleistocene landforms is on-lapped by mud of the central estuarine lagoon. A shore-parallel dune barrier to the west bars and retreats over muddy sediments of this estuarine lagoon. Deltaic complexes invade the southern estuary, with the Collie delta recording a deltaic sand wedge capped by muddy sediment, and the Preston River delta recording a tidal-deltaic system of shifting shoals and mud. At finer scales, the west coast of the estuary (with its staggered dune encroachments) exhibits more complex stratigraphic relationships, and the deltas exhibit complexity of layered sand, muddy sand and mud in upper deltaic sequences, with shoestrings of sand (cheniers) interspersed with muddy sediments, and ribbons and shoestrings of mud.

Within the estuary, sedimentary patterns are underpinned by geomorphology (Fig 8; and Semeniuk 2000). The central basin and northern basin are underlain by bioturbated mud, the eastern platform is underlain by sand, the western platform is underlain by sand, muddy sand and mud (depending on the relationship of dune sand encroaching into the estuary), high-tidal platforms are underlain by root-structured mud, spits and bars-and-lagoons are underlain by sand, muddy sand, mud, and peat, pocket beaches are underlain by sand and shell grit, and the deltas are underlain by complexes of sand, muddy sand, mud and peat. The variety of sediment types and sedimen-

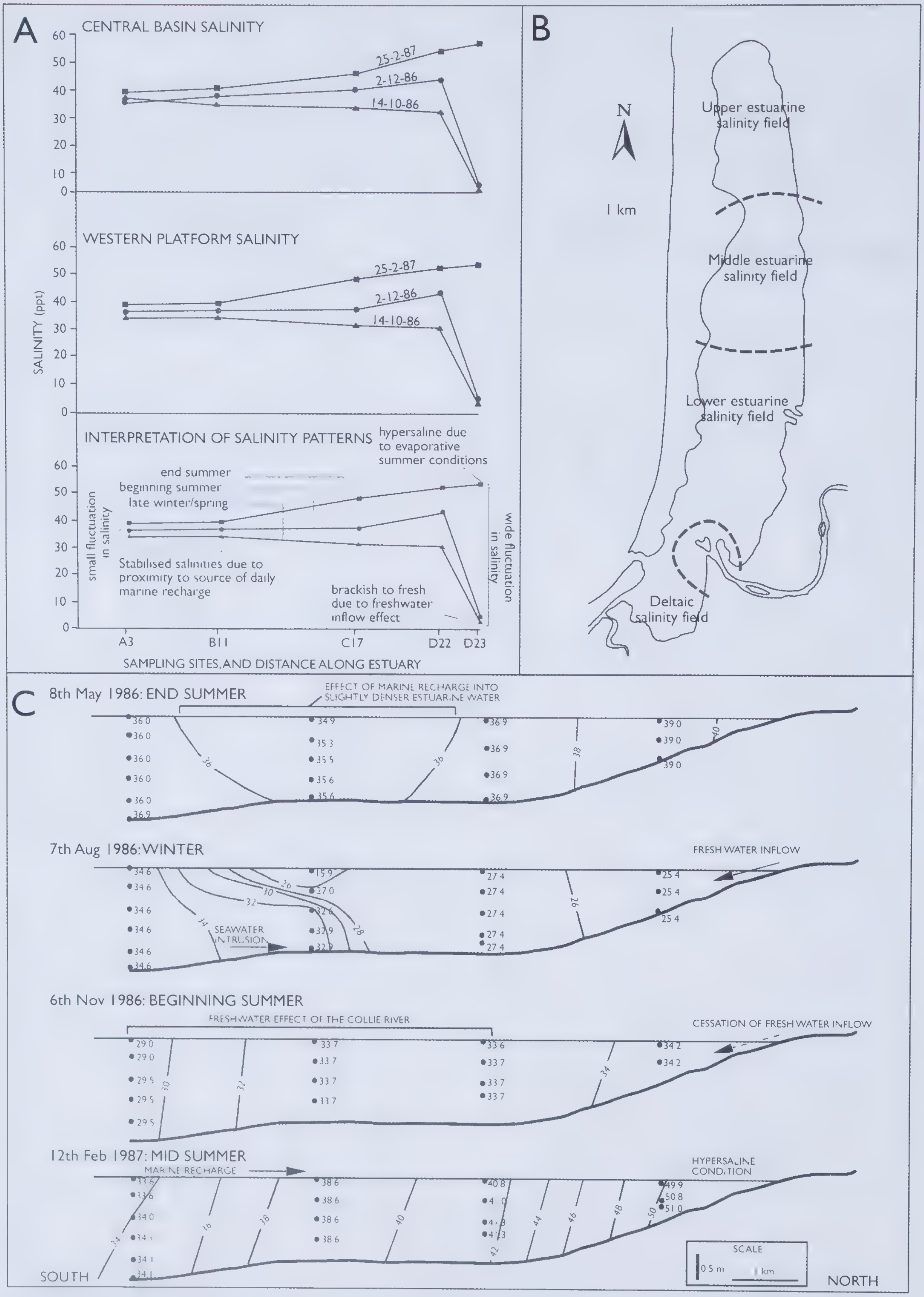

Figure 7. Aspects of the salinity of the Leschenault Inlet estuary. **A:** Salinity of the estuary in the central basin and platform, and interpretation of the trends (modified from Wurm & Semeniuk 2000). **B:** The salinity fields from south to north along the estuary (modified from Wurm & Semeniuk 2000). **C:** South to north salinity profiles and interpretation of dynamics for various seasons 1986-1987 (unpublished data from Wurm & Semeniuk 1986/1987).

tary structures are related to several factors: the nature of the shores that provide reworked material (*e.g.* quartz sand of the eastern shore *vs* quartz and carbonate sand of the western shore), local hydrodynamics (*e.g.* below wave base and thus mud-accumulating, as in the central basin; or predominately wave agitated and hence mud-free sand, as in the eastern platform), and the type of biota as related to environmental conditions.

Hydrological seepages

The Leschenault Peninsula barrier is underlain by dune sand, in turn underlain by muddy to sandy estuarine sediment. Along the estuarine shore, stratigraphic relationships between these sediments are complex. Dune sand fingers extend into muddy environments of the estuary, and muddy sediments accumulate between dune promontories to develop a laterally alternating system of dune sand bodies and muddy sand or mud, each with different hydrologic properties. The barrier separates oceanic water from estuarine water, but beneath the barrier there is a prism of fresh groundwater, with a saline/freshwater interface on both the ocean and estuarine side (Semeniuk & Meagher 1981b). During winter and spring, there is a marked hydraulic head between the fresh groundwater table and marine/estuarine waters, and freshwater discharges into lowlands and adjoining tidal zones as surface seepages (Cresswell 2000). All discharges are pronounced during low tides, especially during equinoctial tides. The consequences of these freshwater discharges are: linear seepage lines along the upper estuarine shore, inhabited by *Juncus kraussii*; more localised, intense discharges inhabited by *Avicennia marina* or by *Melaleuca rhaphiophylla*; and local freshwater to brackish pools in high tidal marshes, which are used by avifauna and mammals.

Peripheral vegetation

Leschenault Inlet estuary is a classic "classroom" for student studies and ecological research of estuarine peripheral vegetation, and it ranks as one of the most significant along the coast of the Swan Coastal Plain (Pen *et al.* 2000). There is a complex of shore types and wetland types peripheral to the estuary (Fig 9). Factors influencing development of these include ancestral landform (*e.g.* the eastern shores), dune dynamics (along the western barrier dune shore), hydrodynamic processes, estuarine coastal processes and sedimentation, and a variable Holocene sea level history. The resulting peripheral estuarine habitats, and salinity gradients therein have resulted in a range of vegetation distributed in mosaics and zones along the shore. The habitats include supratidal flats (samphire-vegetated), high tidal platforms (samphire- or rush-vegetated), tidal embayments (residing between dune corridors), zones of freshwater seepage at interfaces between high tidal platforms and dunes (rush-vegetated), cliffed sandy shores (coastal erosion of dunes), steep dune shores (where dunes are encroaching into the estuary), beachridges, spits, bar-and-lagoon complexes, stranded (relict) sand platforms, and the Collie River and Preston River deltas.

Based on vegetation structure, composition, salinity tolerance, and proximity to shore, five types of vegetation are recognised fringing the estuary (Pen *et al.* 2000). There is saltmarsh, comprising samphires and rushes (dominated by *Halosarcia* spp, *Sarcocornia quinqueflora*, *Frankenia pauciflora*, *Juncus kraussii*, amongst others) developed in saline tidal areas. Estuarine fringing forests, typically of small saltwater sheoak (*Casuarina obesa*), saltwater paperbark (*Melaleuca cuticularis*), paperbark (*Melaleuca viminea*), and swamp paperbark (*Melaleuca rhaphiophylla*) inhabit areas where the elevation increases and soilwater salinity is not extreme. There is fringing vegetation consisting of emergent species living more or less permanently in shallow water (*e.g. Schoenoplectus validus*). Sandy rise vegetation occurs on the crest of sand bars, on margins of high coastal sand dunes, or on low estuarine beach dunes. Freshwater vegetation (forest and disturbance-related types) inhabit areas close to the estuary in areas receiving substantial freshwater input.

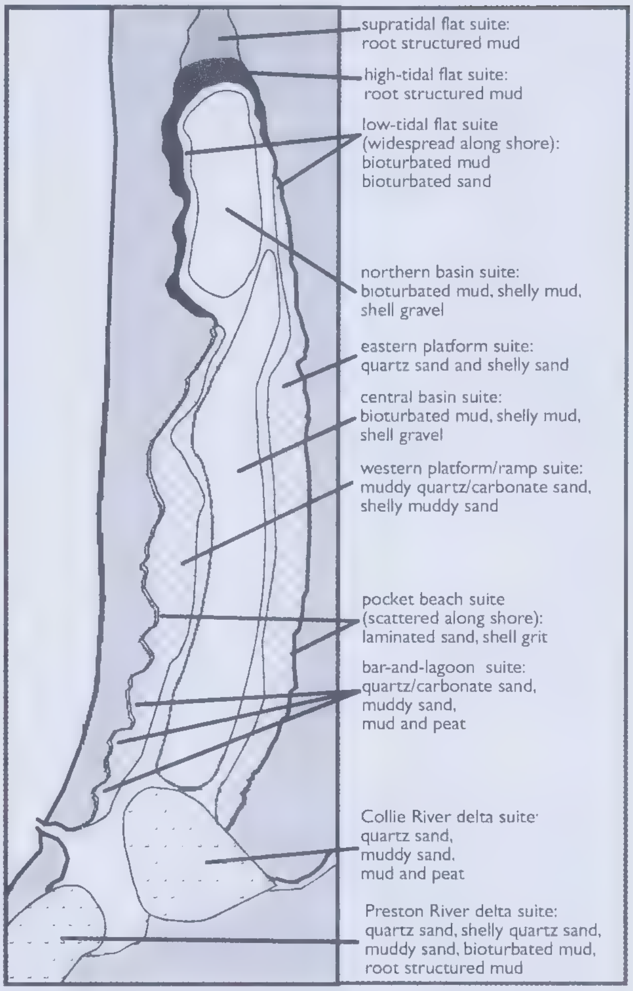

Figure 8. Sedimentary patterns in the Leschenault Inlet estuary showing the main sediment types in the various facies.

White mangrove *Avicennia marina*

Avicennia marina forms scrub, heath, or shrubland in three settings, illustrating different relationships to geomorphic setting and salinity (Fig 9). It is best developed in the marine Preston River Delta where there is daily tidal exchange. It forms scattered shrubs in the upper estuary, inhabiting high tidal platforms, and forms a local copse adjoining a steep dune front where there is fresh water seepage. Population structures of *Avicennia* show polymodality with adult-dominated varying to seedling/sapling-dominated populations at different locations. Changes in mangrove distribution and density have occurred over time *viz* an increase of mangroves both in the Preston River Delta and in front of the steep dune shore, and establishment of small shrubs/saplings on high tidal platforms.

Avicennia in this region is scientifically important as the most southerly occurrence of the species in Western Australia. Semeniuk *et al.* (2000a) present hypotheses to explain this occurrence, ranging from a once widespread coastal distribution and then contraction to this region during the latter Holocene, to being only a recent arrival to the estuary, linked to the Leeuwin Current. Palynology supports the idea that *Avicennia* is only a recent arrival to the region.

Pollen

The Leschenault Inlet estuary is a unique natural laboratory in Western Australia for palynological research with regard to vegetation source, wind directions, dispersal via estuarine currents, taphonomy, and establishment of pollen assemblage baselines for the various estuarine environments. From a geoheritage perspective, the estuary would rank as significant at a National level. The estuarine system is comprised of north-south trending sedimentary environments and shore-parallel vegetation complexes, with both easterly and westerly winds and two rivers contributing to the pollen influx (Semeniuk *et al.* 2000b). Using family groupings (*e.g.* Chenopodiaceae, Myrtaceae, Casuarinaceae, Gramineae and Restionaceae) and several diagnostic species (*Frankenia pauciflora*, *Olearia axillaris*, and *Lepidosperma gladiatum*), preliminary results show that the major sedimentary environments (*e.g.* saltmarsh, western and eastern subaquatic platforms, and central basin) have characteristic pollen, with gradients in abundance of specific pollen related to proximity of vegetation source and type of transport.

Estuarine tidal to aquatic benthic habitats

Bathymetry and large scale geomorphology (*i.e.* central basin, eastern and western platforms, northern flat, tidal zones, and the Collie River delta), and their associated substrates, in combination with hydrodynamics, estuarine salinity patterns, and aquatic vegetation are used to categorise habitats for benthos (Wurm & Semeniuk 2000). Excluding high-tidal peripheral saltmarsh systems, 19 low-tidal to subtidal estuarine habitats have been recognised (Fig 10). Within the upper estuarine salinity field, there is intertidal mud, intertidal sand, vegetated flat mud, and vegetated flat sandy-mud. The central basin spanning the mid and lower estuarine salinity fields, contains sparsely vegetated basinal mud and sandy-mud. The western platform, spanning the mid and lower estuarine salinity fields, contains intertidal sand, intertidal mud, intertidal muddy-sand, intertidal sandy-mud, vegetated platform muddy-sand, vegetated platform mud, and vegetated platform sand. The eastern platform, spanning the mid and lower estuarine salinity fields, contains intertidal sand, vegetated platform sand, and vegetated platform muddy-sand. The Collie River delta, within the deltaic salinity field, has intertidal sand and shallow water sand. Along the northeastern part of the estuary, there is a tidal limestone platform (cut into Pleistocene Kooallup Limestone), veneered by mud; the mud is periodically stripped off by waves, locally exposing the platform.

Seagrasses and aquatic algae

At least 3 species of seagrass and 7 species of algae occur in the estuary (Hillman *et al.* 2000; Wurm & Semeniuk 2000). Seagrasses include *Halophila ovalis, Ruppia megacarpa* and *Heterozostera tasmanica.* Algae include *Chaetomorpha linum*, *Gracilaria* spp, *Ulva* sp, 2 species of Phaeophyta (including *Hormophysa triquetta*), and *Acetabularia* sp Macrophyte distribution and abundance appears determined by depth, substrate and salinity field. Hillman *et al.* (2000) found a total plant biomass generally of 3 000-5 000 tonnes dry weight, with a maximum in spring, with large differences in biomass of seagrass and macroalgae between their individual surveys. Seagrass and total macroalgal biomass, however, appear relatively stable in the medium term. The greatest biomass was noted for *Halophila ovalis*-dominated platforms (Fig 9). *Halophila ovalis* is the most widespread species in the estuary, inhabiting western and eastern platforms, and the subtidal muddy northern flat. *Ruppia megacarpa* inhabits shallow intertidal depressions. *Gracilaria* also is relatively abundant, particularly in the southern estuary, and drifts occur on otherwise bare mud in most peripheral and intertidal portions of the northern flat. *Chaetomorpha* variously covers shallow water mud areas, and *Chaetomorpha* and brown algae are common towards the northern eastern platform. *Acetabularia* inhabits sandy substrates of the eastern shores of the northern flat. Hillman *et al.* (2000) conclude the aquatic flora of this estuary to be similar to other south-western Australian estuaries, but with a relatively high diversity of red algae, and *Hormophysa triquetra* as the dominant brown alga.

The leaves of *Halophila* have encrusting epibionts that include bryozoa, sepulid worms, other tubular worms, egg cases, and diatoms. Faunal epibiota are not common, but diatoms are locally very dense.

Phytoplankton and zooplankton

Hosja & Deeley (2000) show that marine and estuarine diatoms dominate the phytoplankton community in the estuary for most of the year. Bacillariophyta and Dinophyta were most abundant throughout the year, with Cryptophyta and Cyanophyta additionally present mainly in the winter months. The most abundant taxa include *Skeletonema costatum, Rhizosolenia setigera, Chaetoceros perpusillum, Chaetoceros didymum, Chaetoceros straightout, Chaetoceros* sp and *Nitzschia closterium.* Spatial and temporal variability in phytoplankton densities and species numbers occurred throughout the estuary, and short-term blooms were observed during autumn and spring. Species with affinity for freshwater were observed during winter and included diatoms, dinoflagellates, cyanophytes and cryptophytes, and were probably transported into the estuary by winter runoff. There was a high proportion of normally benthic or epiphytic species in surface waters reflecting very shallow depths and significant wind mixing in the estuary. Some species were attached to seagrass

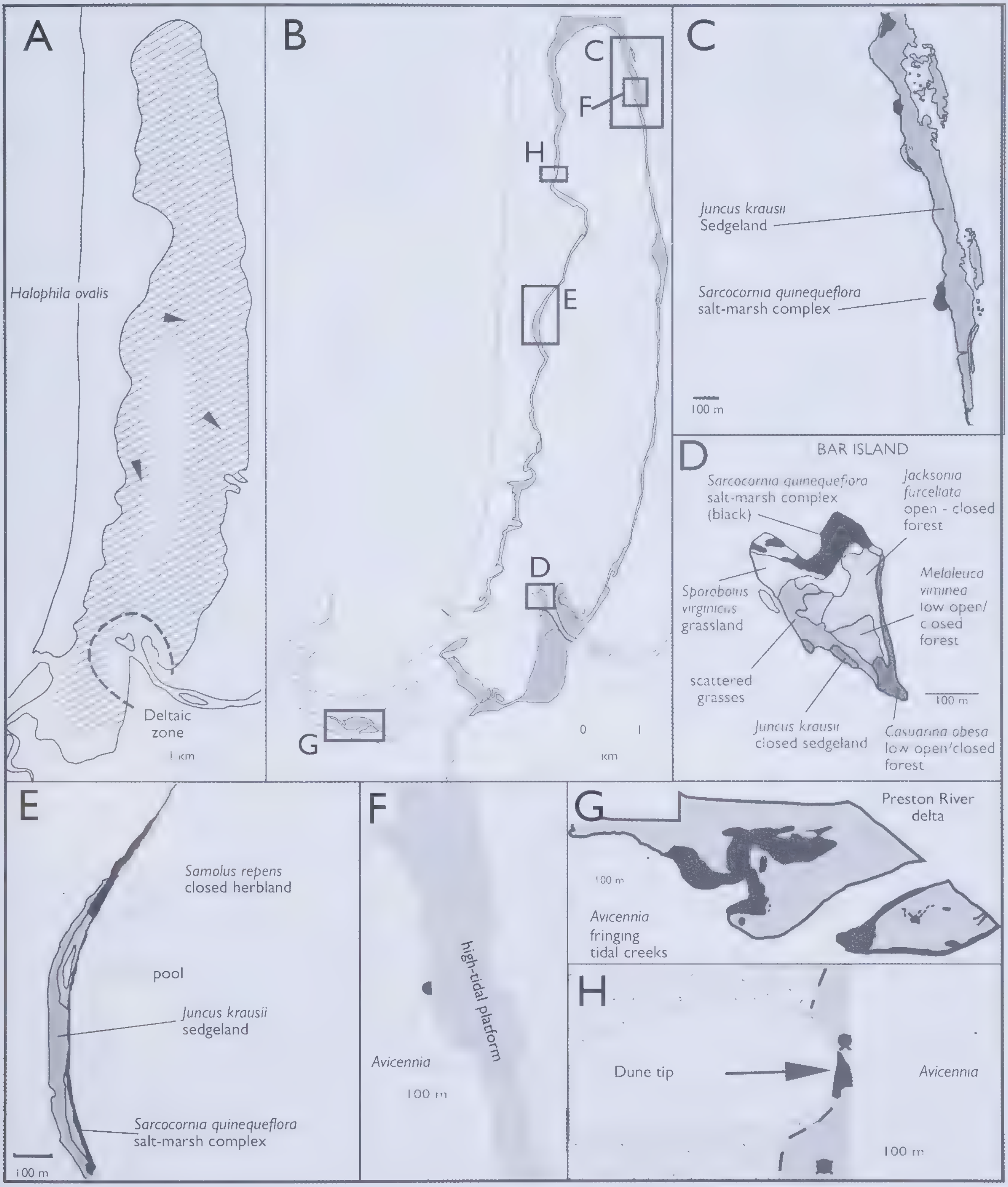
A
Halophila ovalis
Deltaic zone
1 km
B
C
F
H
E
D
G
0 1
km
C
Juncus krausii Sedgeland
Sarcocornia quinequeflora salt-marsh complex
100 m
D
BAR ISLAND
Sarcocornia quinequeflora salt-marsh complex (black)
Jacksonia furcellata open - closed forest
Sporobolus virginicus grassland
Melaleuca viminea low open/closed forest
scattered grasses
100 m
Juncus krausii closed sedgeland
Casuarina obesa low open/closed forest
E
Samolus repens closed herbland
pool
Juncus krausii sedgeland
Sarcocornia quinequeflora salt-marsh complex
100 m
F
high-tidal platform
Avicennia
100 m
G
Preston River delta
100 m
Avicennia fringing tidal creeks
H
Dune tip
Avicennia
100 m

Figure 9. A: Distribution of *Halophila ovalis*, the main seagrass species in the Leschenault inlet estuary, after Lukatelich (1989), located mainly on the shallow water platforms and their slopes that descend to the central basin. **B:** Distribution of estuarine peripheral vegetation in 1989 (from Pen *et al* 2000); insets show more detailed maps. C, D, & **E:** Details of vegetation types along selected portions of the estuarine shore (simplified from Pen *et al* 2000). F, G & **H:** The three setting for *Avicennia marina* in the area (from Semeniuk *et al* 2000b). **F:** shows mangrove shrubs at edge of high-tidal platform. **G:** mangrove distribution in the Preston River delta. **H:** mangrove located at the tip of a dune encroaching into the estuary.

leaves, the most abundant included *Acnanthes*, *Cocconeis*, *Gramatophora*, *Mastogloia* spp, *Paralia sulcata*, and *Synedra* spp. Changes in composition occurred from south to north.

Zooplankton was sampled during summer by Hosja & Deeley (2000) to identify dominant organisms, which included *Sulcanus conflictus*, *Acartiura*, 3 species of Cyclopoid, 2 species of Copepod, 2 species of Calanoiods, 3 species of Hapacticoids, polychaete larvae, *Naupius* larvae, and Malacostraca.

Foraminifera

The foraminiferal fauna of the Leschenault Inlet estuary is exceptional (Revets 2000), with extremely high diversity, exceeding that in most normal marine environments: 118 species were recorded from a total of 1435 specimens examined. Reworking and relict faunas does not explain this diversity. Diversity decreases from south to north, as environments change from stable marine to more extreme conditions, and from east to west, reflecting an increase in contributions of porcellaneous taxa to the overall species spectrum, with a reduction in numbers and diversity of hyaline taxa. The foraminiferal fauna is benthic, and indicative of shallow water. Revets (2000) found the dominant species to be *Ammonia tepida*, followed by *Paratrochammina challengeri* and *Parrellina hispidula*. Planktonic taxa are absent, signaling no significant transport from the ocean into the estuary. With the exception of a single *Planorbulina acervalis*, encrusting forms also are absent, with *Halophila ovalis* seagrass leaves showing no foraminiferal epibionts. Foraminifera typically associated with marginal environments, such as *Ammotium salsum*, *Jadammina macrescens* and *Miliammina fusca* also were absent.

Molluscs

Thirty one species of shelly mollusc, and one unidentified nudibranch, have been recorded in the estuary (Semeniuk & Wurm 2000). These were classified as true estuarine (*e.g. Acteocina* sp, *Xenostrobus securis*, *Hydrococcus brazieri*, *Fluviolanatus subtorta*, *Assiminea* sp, *Salinator* sp), euryhaline marine (*e.g. Tellina deltoidalis*, *Tellina* sp, *Theora lubrica*, *Sanguinolaria biradiata*, *Philine angusi*, *Nassarius burchardi*, *Bedeva paivae*, *Spisula trigonella*, *Epicodakia* sp, *Laternula creccina*), and stenohaline marine (*e.g. Bittium granarium*, *Mytilus edulis*, *Polinices conicus*, *Pholas australasiae*, *Nassarius nigellus*, *Solemya australis*, *Irus crenata*, *Venerupis anomala*). Only seven mollusc species were common in the estuary *viz Arthritica semen*, *Tellina deltoidalis*, *Nassarius burchardi*, *Spisula trigonella*, *Hydrococcus brazieri*, and *Acteocina* sp, and *Bedeva paivae* (Fig 11), inhabiting tidal sand or tidal mud, shallow water platform sand or muddy sand, or deep water basin mud, within lower, middle or upper estuarine salinity fields (Fig 12A). Five years of sampling show the longevity and variability of the molluscan assemblages (Fig 13; Semeniuk & Wurm 2000). The overall character of mollusc assemblages remained similar, but with changes in composition inter-annually and intra-annually: some species were consistently present, though abundance varied seasonally, while others fluctuated markedly, varying from absent to present. Abundance for a given species often fluctuated independently of others and did not appear to reflect patterns in oxygen concentration, temperature or salinity. Many species decreased in abundance over the study period (Cresswell *et al.* 2000). Population structures investigated for *Spisula trigonella*, *Tellina deltoidalis*, and *Nassarius burchardi* over 5 years show *Spisula* populations to be numerically dominated by one age cohort, and not maintained by further recruitment, *Tellina* populations to be maintained by a relatively continuous seasonal low level juvenile recruitment, and *Nassarius* populations to be dominated by a mature age cohort, with a low level intermittent juvenile recruitment.

Small benthic and epibenthic crustaceans

Twenty one species of small benthic and epibenthic crustacea were recorded for the Leschenault Inlet estuary from 1982-1997 (T A Semeniuk 2000). The most abundant species were the isopod *Tanais* sp nov and the amphipod *Corophium* sp (Fig 11). Spatial distributions of crustacean species, encompassing isopods, amphipods, and small crabs, appear to be linked to salinity patterns or to the presence of aquatic vegetation (Fig 12 C). A few species showed preference for particular substrates or depths. Crustacean populations typically showed seasonal unimodal peaks in numbers during summer, with densities typically an order of magnitude greater than winter densities (Fig 13). The magnitude of summer recruitment varied annually for most species, linked to favourable environmental conditions. Changes in population density and distribution were likely linked to adult migration and juvenile recruitment. Over the five years of study, there was an overall decline in abundance of the main species and changes in species composition, signaling a long-term environmental change within the estuary. Hass & Knott (2000), in reporting on sphaeromatid isopods in the area, note that two of the species may have been introduced, most likely by recreational boats.

Blue swimmer crab

The Blue swimmer crab, *Portunus pelagicus* (Fig 11), is a large benthic carnivore in the estuary and the adjoining marine embayment (Koombana Bay). Spawning period, the timing of immigration and emigration and growth patterns of this crab in the estuary are similar each year (Potter & de Lestrang 2000). The crab releases zoeae in Koombana Bay, rather than in the estuary, during mid-spring to late summer, and while a few recruits enter the estuary, their numbers do not start to rise until the following spring, along with rising salinities and water temperatures. After one year, many females and males have reached moderate size (carapace width *ca* 80-90 cm). During the subsequent winter, with lower salinities and water temperatures, numbers of older crabs (*ca* 18-20 months in age) decrease markedly, with a concomitant rise in numbers in the shallows of Koombana Bay.

Polychaetes

A total of 15 polychaete species have been recorded within Leschenault Inlet (Dürr & Semeniuk 2000). Distributions of the dominant species are linked to environmental factors, particularly salinity, water depth and substrate. Three broad polychaete assemblages characteristic of the different environments can be identified (Fig 12 D). Long-term density changes of the three most common species, *Ceratonereis aequisetis*, *Nephtys gravieri* and *Capitella cf capitata* (Fig 11), followed complex patterns (Fig 13). Population density at many sites typically reached a peak in late summer to autumn, but annual periodicity at the scale of the estuary was not obvious for the overall population density of a given species, because large year-to-year variability at single sites and phase differences between sites probably masked the pattern. Long-term trends for *C. aequisetis* at neighbouring sites showed synchronicity, but no relationship to seasonal variation in abiotic factors, suggesting that spatial and temporal changes in polychaete distribution mostly reflect local environmental conditions.

Ophiuroids

A small cosmopolitan, normally oceanic ophiuroid (a brittle star), *Amphipholis squamata* was recorded at varying times over 17 years (1982-1999) in the estuary (Unno 2000). Between 1982-1987, *A. squamata* formed sporadic low density populations in restricted habitats (Fig 12 B), mostly near the boundary of the middle to upper estuarine salinity fields, in well-oxygenated water, with mud to muddy sand substrates, and with usually some seagrass or algae. At specific times (August 1984, September 1986 to March 1987, and October 1990), ophiuroid populations were extremely dense, with the main population located at the boundary of the middle to upper estuary, but with outliers to the north and south.

Fish fauna

Potter *et al.* (2000) describe the fisheries in the Leschenault Inlet estuary, the marine Koombana Bay, and estuarine reaches of the Collie River. Forty two species of fish were recorded from these nearshore and shallow waters in 1994. The most abundant species were the long-finned goby *Favonigobius lateralis*, the sandy sprat *Hyperlophus vittatus* and the atherinids *Leptatherina presbyteroides* and *Atherinosoma elongata* (Fig 11). Twenty of the 42 species were marine, using the estuary as a nursery area (marine estuarine opportunists), and thirteen complete their life cycles within the estuary. The composition of the fish fauna of the shallows of the estuary differs markedly from that of shallow waters in Koombana Bay. The most abundant species in Koombana Bay, the flathead sandfish *Lesueurina platycephala*, was never recorded in the estuary. Fish catches in the deeper estuarine waters include larger species dominated by marine estuarine opportunists and the Perth herring *Nematalosa vlaminghi*. Fish in the Collie River comprised far more species and relatively greater numbers of teleosts, such as yellow-eye mullet (*Aldrichetta forsteri*), tailor (*Pomatomus saltatrix*) and Australian herring (*Arripis georgianus*), and greater numbers of Perth herring and sea mullet (*Mugil cephalus*). The main commercial species in the estuary are *Aldrichetta forsteri*, *M. cephalus*, *S. schomburgkii* and *N. vlaminghi*. The recreational fishery was dominated by three species of whiting (*S. punctata*, *S. schomburgkii* and *Sillago burrus*) and *P. saltatrix*.

The most abundant species were classed by Potter *et al.* (2000) into 5 categories of feeding modes. These are herbivores feeding mainly on algae associated with seagrass (*e.g. Hyporhamphus melanochir*, *Pelates sexlineatus*), and detritivores (*e.g. M. cephalus*, *N. vlaminghi*). Omnivores feed on algae and a range of invertebrates (*e.g. A. forsteri*, *Amniataba caudavittata*). Lower order carnivores feed on small benthic invertebrates (*e.g. A. elongata*, *F. lateralis*, *L. presbyteroides*, *S. punctata*, *S. schomburgkii*, *Torquigener pleurogramma*). Higher order carnivores feed on larger and more active invertebrates and fish (*e.g. Argyrosomus japonicus*, *P. saltatrix*).

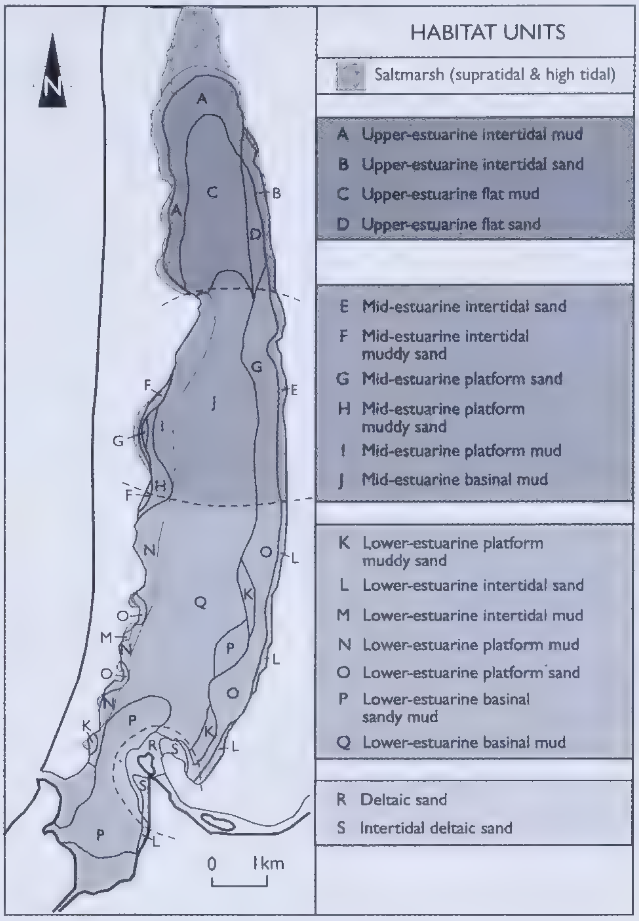
N
HABITAT UNITS
Saltmarsh (supratidal & high tidal)
A Upper-estuarine intertidal mud
B Upper-estuarine intertidal sand
C Upper-estuarine flat mud
D Upper-estuarine flat sand
E Mid-estuarine intertidal sand
F Mid-estuarine intertidal muddy sand
G Mid-estuarine platform sand
H Mid-estuarine platform muddy sand
I Mid-estuarine platform mud
J Mid-estuarine basinal mud
K Lower-estuarine platform muddy sand
L Lower-estuarine intertidal sand
M Lower-estuarine intertidal mud
N Lower-estuarine platform mud
O Lower-estuarine platform sand
P Lower-estuarine basinal sandy mud
Q Lower-estuarine basinal mud
R Deltaic sand
S Intertidal deltaic sand
0 1km

Figure 10. Habitat units in the Leschenault Inlet estuary (modified from Wurm & Semeniuk 2000). The upper, middle, lower and deltaic fields are coded in decreasing shades of grey for ease of referring to the habitat units therein.

Avifauna

As a large, permanent water body with a mixed array of habitats, the Leschenault Inlet estuary supports significant waterbird populations. From nine waterbird surveys conducted over 1987 and 1988, some 23 565 waterbirds, comprising 57 species, were recorded from the estuary, its fringing wetland areas, and in some closely associated outlying wetlands (Raines *et al.* 2000). The five most abundant species were (Fig 11): the Red-necked Stint (*Calidris ruficollis*), the Little Pied Cormorant (*Phalacrocorax sulcirostris*), the Silver Gull (*Larus novaehollandiae*), the Black Swan (*Cygnus atratus*), and the Grey Teal (*Anas gracilis*). The noticeable waterbirds along the saltmarsh shore (Fig 11) are the Great Egret (*Ardea alba*) and the White-faced Heron (*Egretta novaehollandiae*). Waterbirds extensively use most habitats within the estuary and outlying wetlands,

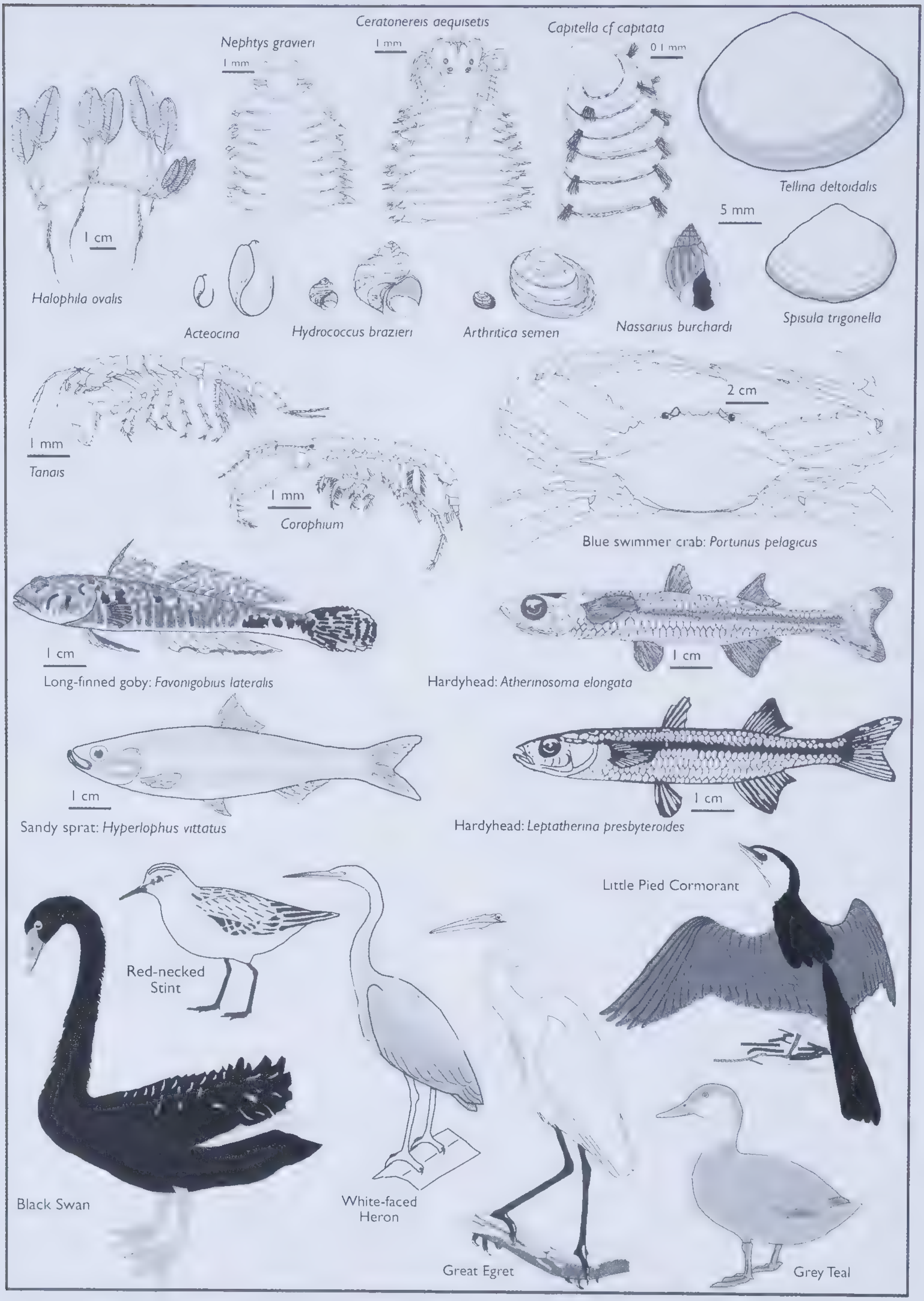

Figure 11. The most common flora and fauna in the Leschenault Inlet estuary. Crustaceans, polychaetes, fish, avifauna, and some molluscs redrawn with modifications from the following sources: Allen (1982), Barnard & Karaman (1991), Boeggemann (1997), Holdich & Jones (1983), Hutchings & Glasby (1985), Hutchins & Thompson (1983), Rainer & Hutchings (1977), Simpson & Day (1996), and Wells (1984). Bar scales are marked for the various species except the avifauna, which mostly are large species (however, the Red-necked Stint is 15 cm in size). While the molluscs relate to a single 5 mm bar scale, the small molluscs are drawn at two sizes; the smaller drawing relates to the bar scale, and the larger drawing illustrates detail.

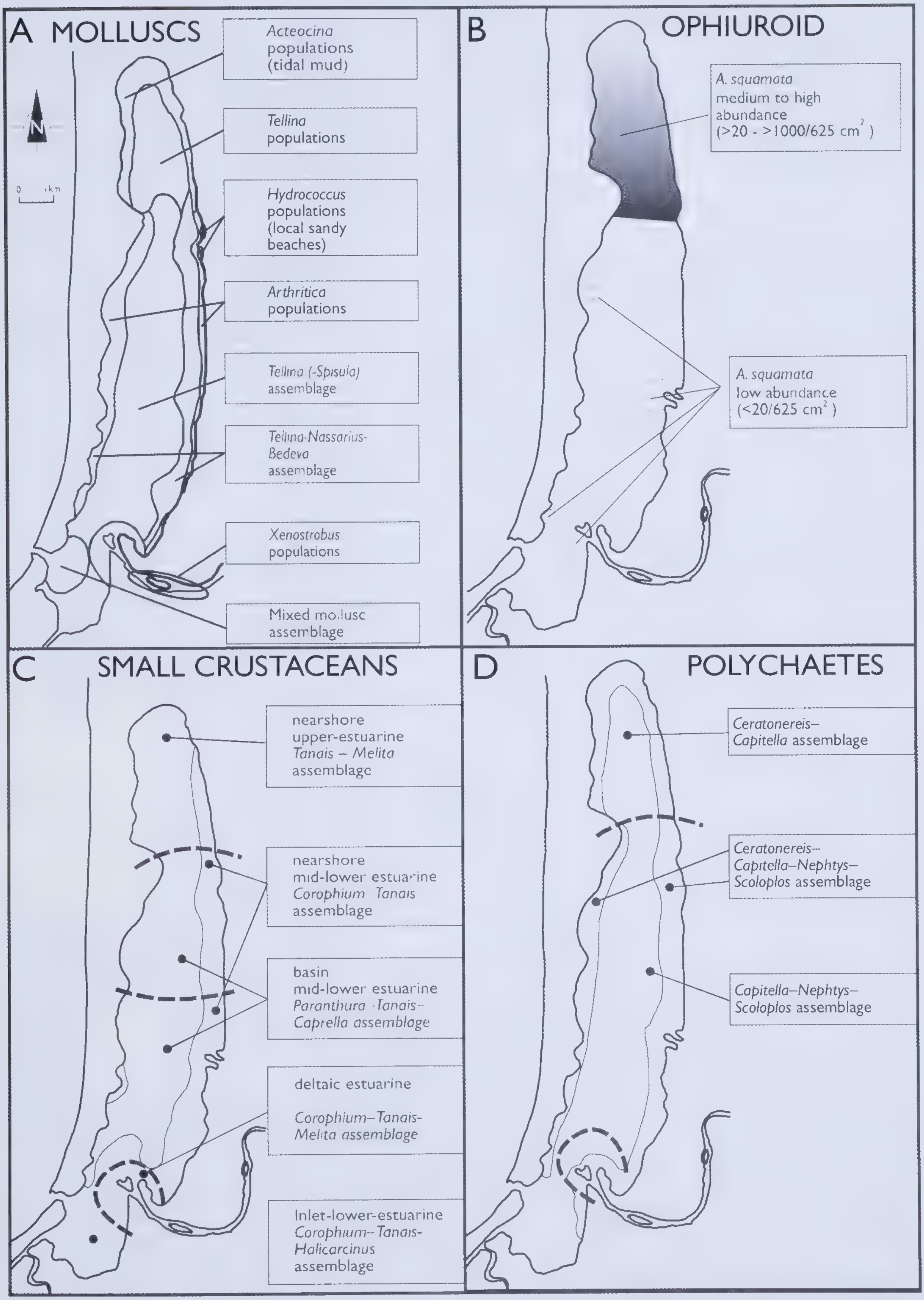
A MOLLUSCS
N
0 1km
Acteocina populations (tidal mud)
Tellina populations
Hydrococcus populations (local sandy beaches)
Arthritica populations
Tellina (-Spisula) assemblage
Tellina-Nassarius-Bedeva assemblage
Xenostrobus populations
Mixed mollusc assemblage
B OPHIUROID
A. squamata medium to high abundance (>20 - >1000/625 cm²)
A. squamata low abundance (<20/625 cm²)
C SMALL CRUSTACEANS
nearshore upper-estuarine Tanais – Melita assemblage
nearshore mid-lower estuarine Corophium Tanais assemblage
basin mid-lower estuarine Paranthura -Tanais-Caprella assemblage
deltaic estuarine Corophium–Tanais-Melita assemblage
Inlet-lower-estuarine Corophium–Tanais-Halicarcinus assemblage
D POLYCHAETES
Ceratonereis–Capitella assemblage
Ceratonereis–Capitella–Nephtys–Scoloplos assemblage
Capitella–Nephtys–Scoloplos assemblage

Figure 12. Occurrence of key benthic faunal assemblages and populations in the estuary (data from Semeniuk & Wurm 2000; TA Semeniuk 2000; and Dürr & Semeniuk 2000).

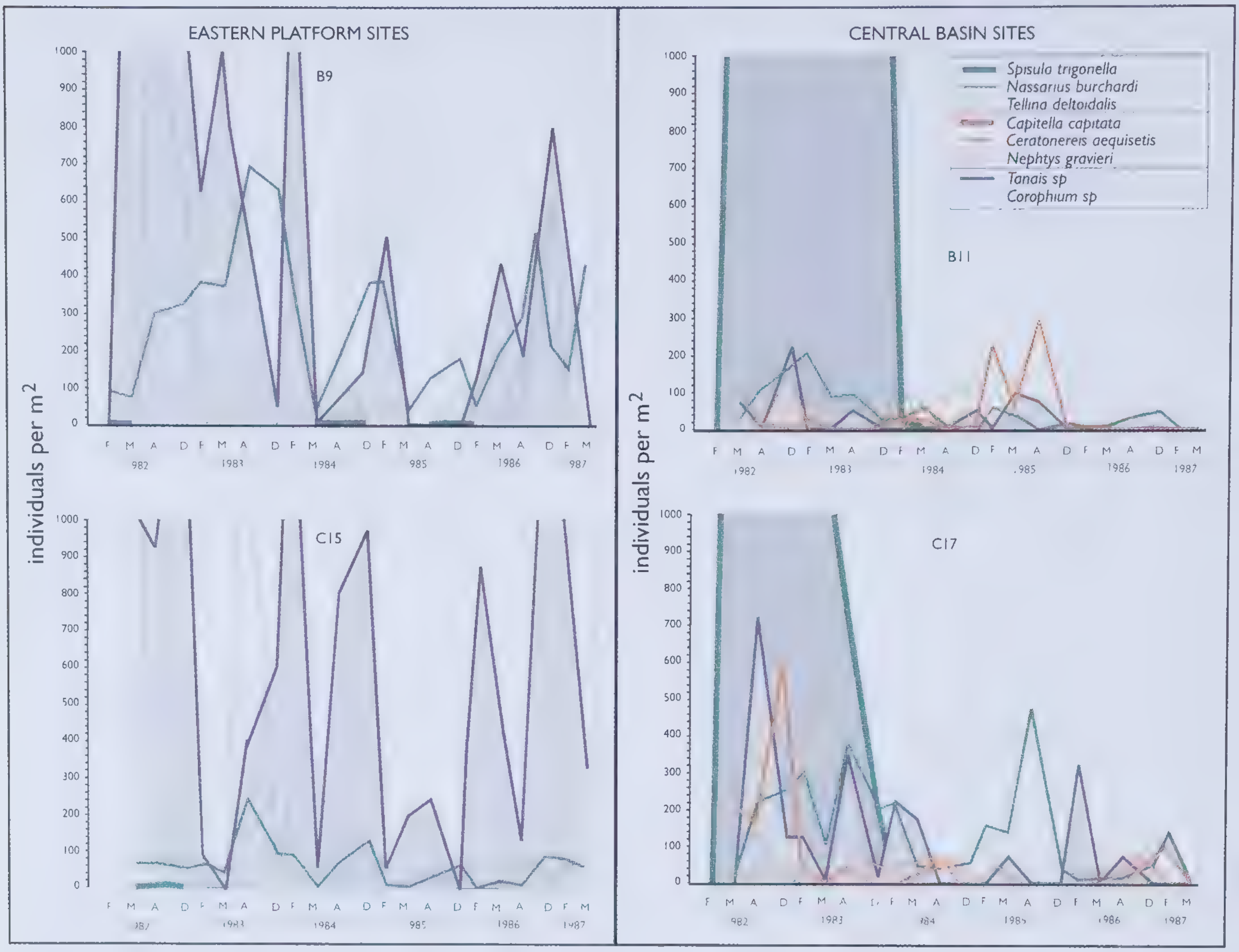

Figure 13. Temporal variation in key species of invertebrate fauna during the period 1982-1987 for selected sampling sites in the estuary (data from Semeniuk & Wurm 2000; TA Semeniuk 2000; and Dürr & Semeniuk 2000). The sites selected are two eastern platform sites (B9 & C15) and two central basin sites (B11 & C17). The graphs showing the two most abundant species are filled in with grey (*Spisula*) and light grey (*Tanais*) to highlight their patterns and to create a backdrop against which to view the other species.

often for different purposes. Open-water habitats (the deep-water basin, sandbars and shallow water reaches) support a large part of the waterbird population (including Little Black Cormorant, White-faced Heron, Hoary-headed Grebe, Black Swan and Musk Duck), and are mostly used for feeding. Fringing wetland habitats (wet and dry salt marshes and pools), support a greater density and a larger variety of waterbirds (including Grey Plover, Red-necked Stint, Sharp-tailed sandpiper, Black-winged Stilt and Grey Teal), and are used for feeding, roosting, and breeding.

Raines *et al.* (2000) determined significance of habitats within the estuary and out-lying wetlands by analysing numbers, species richness and behavioural activity of waterbirds in each habitat type. The estuary is an important waterbird location and is likely to be critical in the wetland network used by waterbirds in this region. As a dry season refuge for waterbirds in mid spring and summer, it ranks amongst the top wetlands in south-western Australia in terms of species richness, numbers of waterbirds and numbers and richness of species protected under international migratory bird agreements.

Population dynamics and episodic explosions

Several studies have shown the variable nature and overall trend of biota in the estuary over the medium term (5-20 years). Some species population numbers fluctuated markedly from year to year, as well as intra-annually. Other species showed seasonal fluctuations. A number of mollusc, small crustacean and polychaete species also showed a general decline in abundance over the period 1982-1987. Using data from Semeniuk & Wurm (2000), T A Semeniuk (2000) and Dürr & Semeniuk (2000), relative abundances of the three most common species of mollusc, two most common species of small benthic crustacea, and three most common species of polychaete over the period 1982-1987 are shown for some selected sites (Fig 13). These results show several patterns (Fig 14). There is marked variation in species abundance from site to site. Species that at times show seasonal fluctuations include *Corophium*, *Tanais*, *Tellina*, and *Nassarius*, with some of these species abundant in the winter to post-winter period, and others in the summer. *Tanais*, and some sites for *Tellina* and *Nassarius* show a general decline in population abundance. There were also

Table 2. Comparisons between 1982-1987 and 1998 in environmental conditions and biota for selected sites (sample sites of Wurm & Semeniuk 2000)

Site	Description 1982-1987	Description May 1998	Habitat changes
A5	shallow water platform: dense seagrass cover, moderate to abundant invertebrate fauna	no seagrass, molluscs and benthic small crustacea absent, low abundance of polychaetes	muddy sand habitat remained similar
B9	shallow water platform: dense seagrass cover, moderate to abundant invertebrate fauna	no seagrass, molluscs and benthic small crustacea absent, low abundance of polychaetes	muddy sand habitat remained similar
B11	deep water basin: low to no seagrass cover, generally moderate to low abundance of invertebrate fauna, except for the *Spisula* invasion	no seagrass cover, absence of invertebrate fauna	mud habitat remained similar
B13	shallow water platform: dense seagrass cover, generally moderate to abundant invertebrate fauna	no seagrass, molluscs and benthic small crustacea absent, low abundance of polychaetes	muddy sand habitat remained similar
C16	shallow water platform: dense seagrass cover, moderate to abundant invertebrate fauna	no seagrass, molluscs and benthic small crustacea absent, low abundance of polychaetes	muddy sand habitat remained similar
C17	deep water basin: low to no seagrass cover, generally moderate abundance of invertebrate fauna	no seagrass cover, absence of invertebrate fauna	mud habitat remained similar
C18	shallow water platform: dense seagrass cover, generally moderate to low abundance of invertebrate fauna	no seagrass, molluscs and benthic small crustacea absent, low abundance of polychaetes	original sandy mud habitat now covered in 2-3 cm of mud
D22	shallow water mud flat: patchy algal cover, temporally variable high, moderate to low abundance of invertebrate fauna	no vegetation cover, molluscs absent, low abundance of polychaetes and benthic small crustacea	mud habitat remained similar

episodic increases in population abundance for some species superimposed on any seasonal fluctuations (*viz Capitella, Corophium, Spisula*). For the mollusc data, Cresswell *et al.* (2000) corroborate these patterns mathematically, and conclude that inter-annual variation in molluscan composition is so marked that it would be difficult to categorise biota in terms of consistent assemblages.

To determine the status of the estuary 10 years after the previous detailed invertebrate sampling (between 1982 and 1987), we resampled many of the 22 sites described in Wurm & Semeniuk (2000) in April 1997 and in May 1998. The May 1998 survey concentrated on sampling at least one western platform site, one deep water basin site, and one eastern platform site along the Transects A, B, C, and D. Both the April 1997 and the May 1998 surveys showed seagrass generally to be in low abundance or absent throughout the estuary, molluscs similarly to be in low abundance or absent, benthic small crustaceans (whose abundance is related to seagrass cover) to be generally in low abundance to absent, and polychaetes to be generally present but in low abundance (with an added complication that polychaete species composition had changed; Dürr & Semeniuk 2000). The May 1998 results are summarised in Table 2. Some of the fauna changes may be linked to habitat substrate changes: for example, sandy mud at site C18 of Wurm & Semeniuk (2000), that between 1982 and 1987 was consistently covered in dense *Halophila* with moderate to abundant invertebrate fauna, in May 1998, was veneered by 2-3 cm of

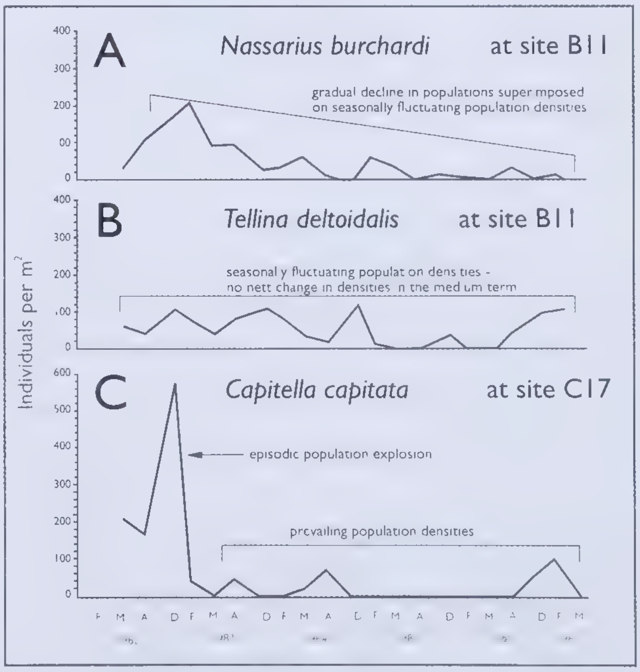

Figure 14. Specific examples derived from Figure 13 of patterns of population abundance for three species. A. Overall decrease in abundance superimposed on seasonal fluctuations in density. B. Seasonal fluctuations in population density. C. Periods of episodic populations explosions amid a prevailing situation of generally low population numbers.

mud, had no seagrass cover, and was depauperate in fauna. However, at other sites there was no change in sediment substrate, but significant change in biota *e.g.* Site A5, that was consistently covered in a dense *Halophila*, with moderate to abundant invertebrate fauna between 1982-1987, in May 1998, though still underlain by muddy sand, had no seagrass cover, and was depauperate in fauna.

In summary, the results from the various invertebrate studies show a general decrease in abundance during the period 1982-1987, commensurate with decreasing biomass of seagrass throughout the estuary over the same period (Hillman *et al.* 2000). Although there was no sampling of invertebrate fauna between 1987 and 1998, Hillman *et al.* (2000) indicate that seagrass was abundant in the estuary over the period 1988-1993, and invertebrate fauna similarly may have been abundant. In April 1997 and May 1998 the estuary was biologically depauperate, with negligible seagrass cover at the sampling sites, and low numbers of invertebrate fauna.

Two of the studies in this Volume describe "population explosions", *viz Spisula trigonella* and the ophiuroid *Amphipholis squamata*. Marked increases in population density are also evident in the *Corophium* and *Tanais*. Between 1982 and 1987, *Spisula trigonella* populations experienced massive juvenile recruitment in early 1983 (the "1983 *Spisula* invasion"), resulting locally in tens of thousands of individuals in a square metre for a short term. The populations then rapidly decreased to low numbers. Prior to this, the species appeared to be in very low abundance when sampled by Chalmer & Scott (1984), although this may have been an artifact of the few sampling sites involved. Similarly, the species mostly was absent with the estuary-wide sampling undertaken by the authors in 1998. The ophiuroid *Amphipholis squamata* also showed marked but episodic increases in population density (Unno 2000). Generally, over 17 years, sporadic low density populations of the ophiuroid were recorded in the estuary, in restricted habitats, but at specific times (August 1984, September 1986 to March 1987, and October 1990), populations were dense.

Anthropogenic impacts

Geographically, the major anthropogenic impacts on the estuary have been (Fig 15): 1. destruction of much of the Preston River Delta through land reclamation, dredging and harbour construction; 2. dredging "The Cut", altering estuarine landforms, hydrodynamics and hydrochemistry; 3. destruction of the southern Collie River Delta through urbanisation; and 4. clearing and drainage of estuarine shores, resulting in changes to the peripheral estuarine vegetation. Four types of impacts can be categorised (Table 3).

Description of the reclamation, modification, dredging and urbanisation of the Preston River and Collie River del-

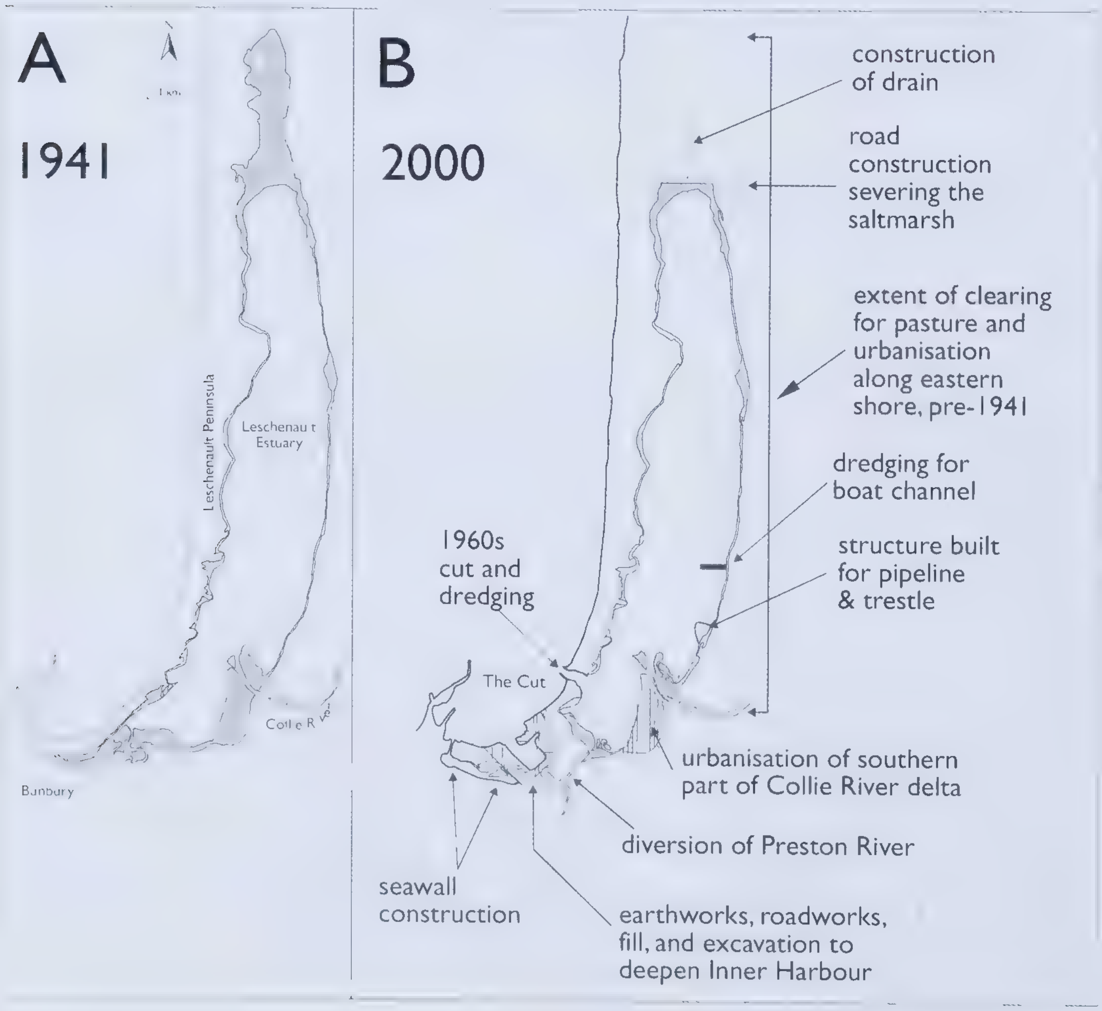
A
1941
1 km
Leschenault Peninsula
Leschenau t Estuary
Coll e R ver
Bunbury
B
2000
construction of drain
road construction severing the saltmarsh
extent of clearing for pasture and urbanisation along eastern shore, pre-1941
dredging for boat channel
structure built for pipeline & trestle
1960s cut and dredging
The Cut
urbanisation of southern part of Collie River delta
diversion of Preston River
seawall construction
earthworks, roadworks, fill, and excavation to deepen Inner Harbour

Figure 15. Types and locations of anthropogenic impacts in the Leschenault Inlet area.

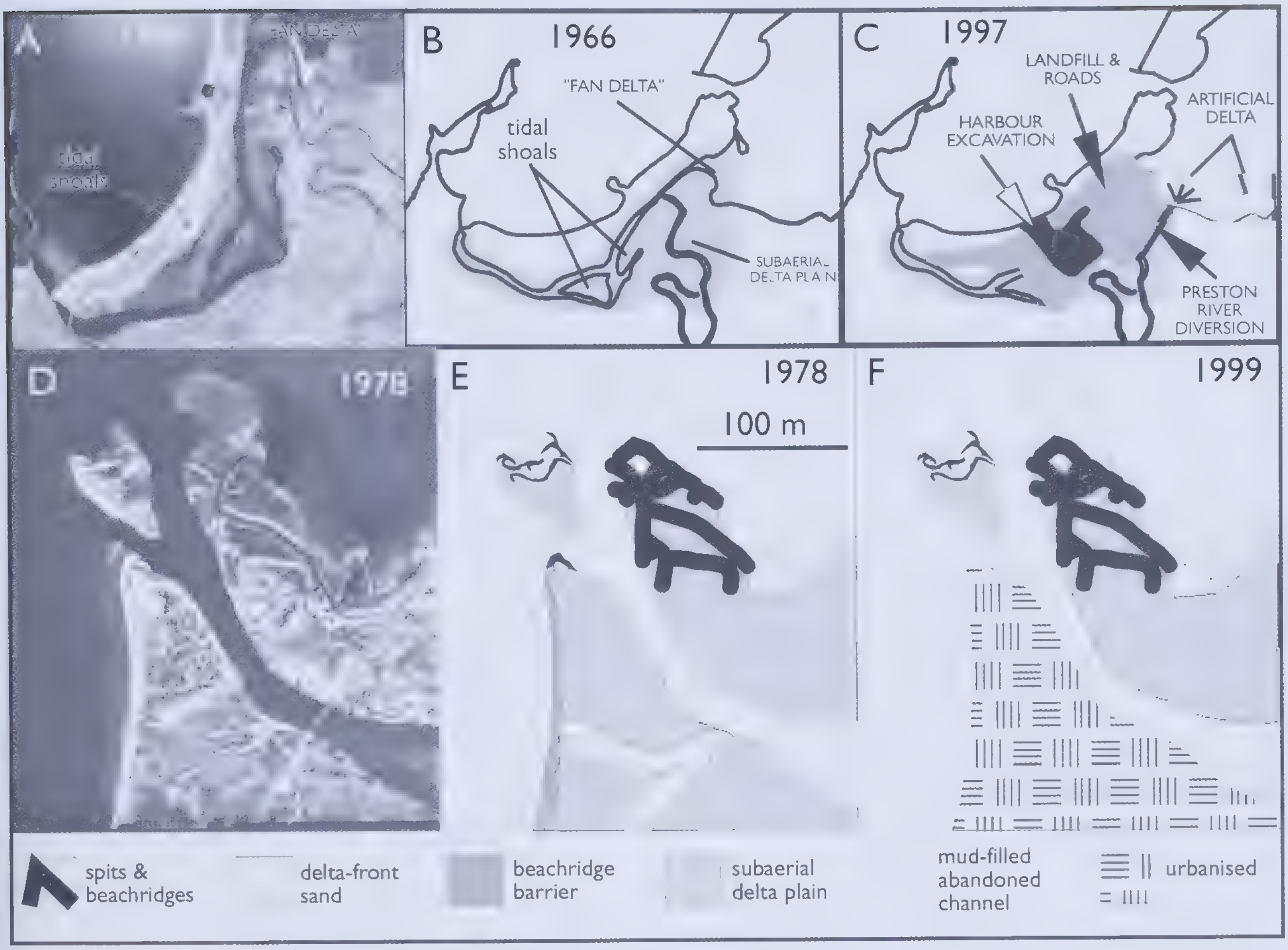

Figure 16. Impacts on the estuarine deltas (A-C: Preston River delta; D-F: Collie River delta). **A:** Aerial photograph of the Preston River delta in 1966, showing tidal shoals, fan delta, and meandering channels on the sub-aerial plain. **B:** Map of the delta in 1966 showing the sub-aerial delta plain, meandering river channels, tidal shoals, and the fan delta. **C:** Four types of anthropogenic impacts on the delta (viz., landfill and roads, harbour excavation, channel diversion, and redirected deltaic sedimentation) largely destroying its integrity by 1997. **D:** Aerial photograph of the Collie River delta in 1978 showing main channel, mid-channel island, cheniers on its northeastern part, sub-aerial plain and abandoned distributary channels on its southern part. **E:** Map of the delta in 1978, showing the geomorphic components. **F:** Map of the delta in 1999, showing extent of destruction of the southern part of the delta through urbanisation.

tas is amplified here and in fig 16, since these geomorphic/sedimentologic features and their vegetation are significant in terms of geoheritage and biogeography (Semeniuk & Semeniuk in press). The deltas in the Leschenault Inlet system comprise the southern part of a dune-barrier-protected elongate shore-parallel lagoon, and both were proximal to the former tidal outlet of the estuarine lagoon. In this context, the Preston River Delta had delta landforms strongly influenced by its tidal setting, resulting in tidal-current oriented deltaic shoals and islands, a type of estuarine delta not present elsewhere in Western Australia. The Collie River Delta, because of its geographic/hydrodynamic setting, has an unusual asymmetry in its internal deltaic landform structure: though overall a fluvially constructed delta and hence forming a projection into the estuary, the delta is beachridge- and chenier-dominated on its northern front facing winter storm waves generated along with the large fetch of the elongate estuarine lagoon, but is fluvial-dominated on its southern front, exhibiting abandoned channels, floodplains and levees.

The deltas of the Leschenault Inlet estuary are/were unlike the estuaries and deltas of the Swan River and other rivers northwards (all of which are shore-normal systems), unlike the Peel-Harvey Estuary, which is a compound type with tidal delta, wave dominated delta and elongate birdsfoot delta (Semeniuk & Semeniuk 1990), and unlike the Vasse-Wonnerup estuarine system which is part of a prograding beach-ridge barrier-and-lagoon complex. Thus, from a State-wide perspective, the assemblage of estuarine and deltaic landforms in the Leschenault Inlet area was unique in central to southern coastal Western Australia. Further, the delta of the Preston River was the main habitat for the most southerly occurrence of the white mangrove *Avicennia marina* (Semeniuk *et al.* 2000b), a feature of State-wide significance.

The Leschenault Inlet estuary currently is mildly nutrient enriched, with nutrient loadings appearing during winter freshwater influx, and related to amount of rainfall and river flow (Anon 1995). The sources of the nutrient are riverine (about 51 tonnes of phosphorous and 610 tonnes of nitrogen enter the estuary annually from such sources; Anon 1995), with contributions from the Collie, Brunswick and Preston

Table 3. Description of impact or effect of the various anthropogenic activities

Activity	Description of impact or effect
Engineering activities	land reclamation and boat harbour construction in the northern Preston Delta; diversion of the Preston River into the (now) southern Leschenault Inlet estuary, and the consequent effects of artificial deltaic sedimentation; dredging and construction of boat harbours, and small to large boat channels; drainage; channeling/dredging of "The Cut" through the Leschenault barrier dune, fundamentally changing the estuarine hydrochemistry and hydrodynamics, and creating a flood tidal delta; landscaping and arresting of dune encroachment, depleting sand supply to the estuary
Alteration of estuarine water quality	nutrient enrichment (fertiliser use) of catchment drainage resulting in influx of nutrients into the estuary; nutrient import from foreshore via fertiliser use and local pastoral activities on the east shore; local contamination through use, storage and leakage of various chemicals and hydrocarbons in the area peripheral to the estuary along its eastern shore
Peripheral land use	clearing for pasture, resulting in nutrient enrichment of water that enters the estuary, and changes in groundwater hydrodynamics and seepage into the estuary; urbanisation resulting in clearing, fertiliser application, and human habitation and consequent destruction of coastal landforms and deltas, nutrient enrichment of water entering the estuary, and changes in groundwater hydrodynamics and seepage into the estuary; drainage alteration
Boating/ fishing	boat wake erosion; fishing for fin-fish; netting for crabs; damage to seagrass beds through anchoring

rivers (Fig 1) that drain farmlands in their catchments, as well as local groundwater seepages contaminated by lawn and garden fertilisers, pasture use, and septic tanks. However, studies on phytoplankton and macrophytes of the estuary suggest that the impact of nutrients on the estuary to date has been small (Hosja & Deeley 2000; McComb *et al*. 2000).

Discussion

The Leschenault Inlet estuary is unique in south-western Australia from many perspectives. It is the only estuary formed behind a shore-parallel dune barrier, and wholly Holocene in age (since all other major estuaries in Western Australia have a Pleistocene ancestry). Its estuarine hydrologic structure also is different to other local, more classic type estuaries such as the Swan River Estuary and the Peel-Harvey Estuary, as there is not a simple river-to-sea gradient, but rather rivers enter at one end of a long coastal lagoon that was not formed as part of a fluvial tract. In this context, the Swan River forms a classic estuary, with an upstream riverine system, and a downstream marine setting, while the Peel-Harvey estuary is a compound estuary of three rivers, with the Serpentine and Murray rivers debouching into Peel Inlet (that was formed as a lowland in the zone of fluvial confluence, Semeniuk & Semeniuk 1990), and the Harvey River forming a delta within a fluvially scoured tract leeward of a Pleistocene limestone barrier. Further, of all the estuaries in south-western to southern Western Australia, Leschenault Inlet estuary has had the most complicated Holocene sea level history, resulting in complexity of its shores. The western shore is further complicated because of the dynamic nature of the parabolic dunes that encroach and spill over into the estuary, producing a varied assemblage of shore types. The varied nature of the shores results in variable types of peripheral vegetation, and as such the peripheral vegetation fringing the estuary ranks as one of the most significant in the State. Additionally, through its proximity to the Leeuwin Current, the estuary supports the most southern occurrence in Western Australia of the mangrove *Avicennia marina*.

From a geoheritage perspective, and archive for Holocene climatic and vegetation history, the array of landforms and vegetation in and around the estuary also combine to create an important classroom for pollen studies. From a perspective of biodiversity, the foraminiferal assemblages in the estuary are unusually species rich for an estuary, and potentially globally significant.

In the period from 1982-1998, when detailed monitoring and periodic resampling were carried out, the estuary appeared to be stable in the medium term; that is, while there have been influxes of sediments that changed the depth and nature of the substrate at two sites (one at the mouth of an active delta, the other along the dynamic western shore), overall the depth and substrate character of the estuary, in terms of sediment types, has remained similar. Any changes in the estuarine biotic assemblages over this period would then implicate medium term (decadal) changes in volume of run-off entering the estuary and hence changes in hydrochemistry and nutrient levels, as well as extra-estuarine recruitment, or interactions between biota as driving forces behind these changes.

Monitoring of biota over the medium term in the Leschenault Inlet estuary shows some important patterns. Benthic fauna and seagrass cover were relatively abundant at the beginning of the biota surveys over the period 1982-1987, and appear to have declined towards 1987. In 1997/1998 seagrass and invertebrate fauna again were in low abundance. The decline in fauna may be linked to the abundance of seagrass cover in the estuary, which in turn may be linked to medium term climatic patterns of relative drought (with the concomitant effect of reduced fluvial input from the drainage basin, and reduced nutrient content noted above). Recruitment and abundance of fauna may also be linked to extra-estuarine conditions linked to oceanographic factors.

The mangrove *Avicennia marina* presents an interesting situation of the slow responses of environments to human impacts. While the "The Cut" was dredged in the early 1960s, and the Preston River delta with its mangroves was transformed in the 1970s to a marine embayment without freshwater influx, the mangrove populations in both Leschenault Inlet (the former Preston River delta) and the now Leschenault Inlet estuary remained relatively stable until the late 1980s (Semeniuk *et al.* 2000b). Thereafter, the mangrove began to expand its populations in the Preston River delta area and in the northern Leschenault Inlet estuary decades after the hydrodynamic and hydrochemical modifications.

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The Leschenault Inlet estuary: physical features and habitats for benthic fauna

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Abstract

The Leschenault Inlet estuary has a distinctive pattern of bathymetry, water salinity and sediment types. The estuary is a flat, elongate central basin, flanked to east and west by shallow, shore-parallel platforms. The central basin grades into a shallow-water flat in the north, and adjoins deltas in the south. The estuary is underlain by mud in the central basin and northern flat, sand and muddy-sand on the eastern platform, mud, muddy-sand, sandy-mud and sand on the western platform, and predominantly sand under the deltas. The estuarine waters undergo seasonal changes in salinity as a result of restricted oceanic exchange, freshwater inflow during winter and evaporation in summer. Various salinity fields were identified in this study, based on the mean and range of salinity values occurring within the annual hydrological cycle. Hypersaline to mesosaline waters occur to the north, and increasingly more hyposaline to mesosaline waters occur to the south. Each of the large-scale geomorphic units in the estuary can further be subdivided on the basis of water salinity, bathymetry, substrate and presence of macrophytes. Based on these physical features, nineteen small-scale habitats units were proposed for Leschenault Inlet. These smaller scale habitat units provide a framework within which to study the distribution and ecology of benthic fauna.

Keywords: estuarine habitat classification, Leschenault Inlet, estuary, south-western Australia.

Introduction

Leschenault Inlet (Fig 1) is one of many estuaries in south-western Australia (Hodgkin *et al.* 1979). However, it is unique in the region as it has developed behind Holocene barrier dunes some 8 000 years ago, and has remained an estuarine lagoon since then (Semeniuk 1985). During its history, the combination of evolving adjacent subaerial landforms, regional climate, fluvial input of fresh water and sediments and restricted oceanic exchange has generated a dynamic and heterogeneous estuarine system. As such, Leschenault Inlet provides an opportunity to investigate a small and well defined system that contains a variety of estuarine features.

Other estuaries in south-western Australia have been studied to varying detail (Spencer 1955; Ashman *et al.* 1969; Smith 1975; Wallace 1975; Chalmer *et al.* 1976; Brown *et al.* 1980; Wells *et al.* 1980; Wells & Threlfall 1981 1982 a,b,c; Lukatelich & McComb 1983; Chalmer & Scott 1984; Hodgkin 1984; Anon 1985a; Semeniuk & Semeniuk 1990, 1991), mostly concentrating on some aspect of biota, geomorphology, hydrology, sedimentation, peripheral vegetation habitats, or age structure of estuaries. Leschenault Inlet was briefly surveyed for benthic fauna in 1974 by Chalmer & Scott (1984), and other workers have reported incidentally on it for comparative biological work (Smith 1975; Wells & Threlfall 1981).

Most of the above studies have focused on the biology and occurrence of specific molluscs, or on the physical features of the Inlet. Previous studies have not generally integrated the information on the features of the estuary into descriptions of habitats for fauna. This study developed a more detailed description of the estuarine environment of Leschenault Inlet than has previously been undertaken. The description of physical features was then used to develop a framework of estuarine habitats within which to consider the distribution and ecology of biota such as molluscs, crustacea, polychaetes, echinoderms, peripheral vegetation, mangroves, and avifauna. Such a framework may also be useful for designing and implementing future sampling programs within the estuary.

Environmental setting of Leschenault Inlet

Climate

Climate has a major effect on Leschenault Inlet, particularly on salinity and wind-induced processes. Salinity changes are due to fresh water input during winter, evaporation during summer, and wind-induced circulation and mixing of water. Wind shapes the large-scale habitats within the estuary (*e.g.* dune encroachment along the west shore), and generates waves and currents which rework substrates, transport sediment, cause turbidity, disperse sand sheets, and form shoreline spits. The climate of this region is typified by mild wet winters and hot dry summers. Annual rainfall is 881 mm, falling mainly between April and August. Annual evaporation is approximately 1 300 mm, and is most extreme in summer. Mean maximum summer temperature is 27.9 °C, and mean minimum winter temperature is 8.3 °C (Anon 1975). Wind patterns are related to summer and winter seasons (Semeniuk & Meagher 1981a). Summer winds are dominated by sea breezes emanating from south-western sectors, and land breezes emanating from SE to NE sectors. Winter is characterized by mild winds usually from easterly sectors, and occasional storms.

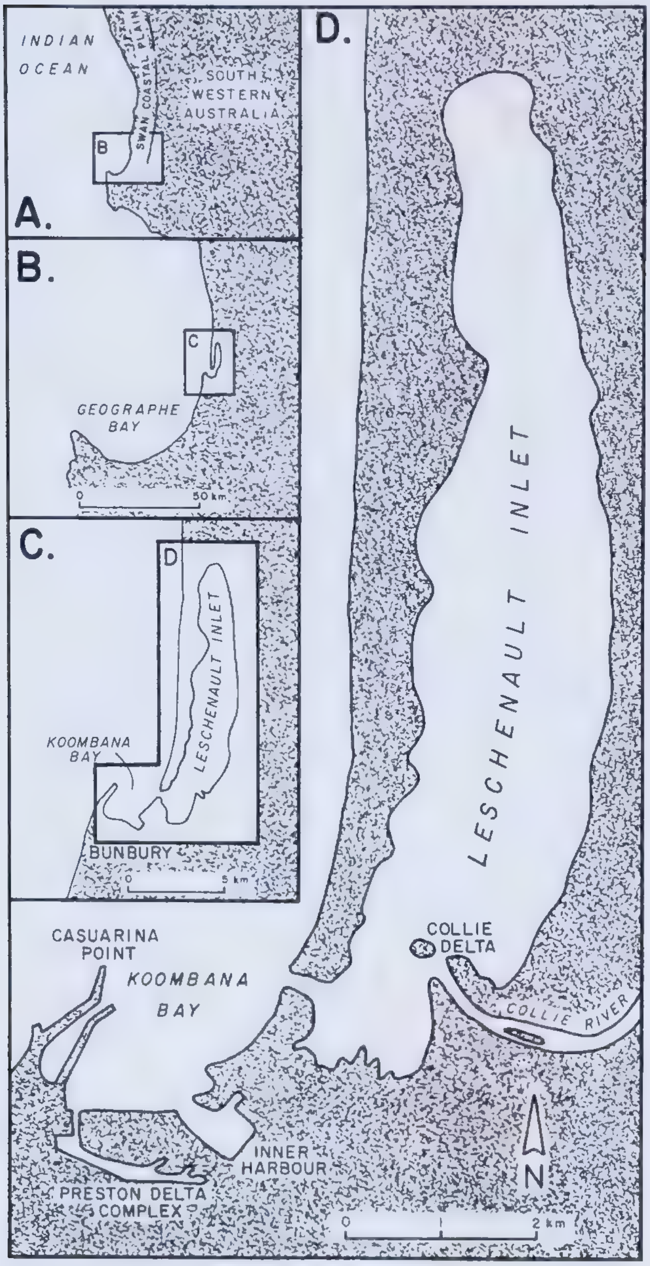

Figure 1. Location of the Leschenault Inlet.

Geomorphology

Leschenault Inlet is located at the junction of Yalgorup Plain, Mandurah-Eaton Ridge, and the Quindalup landform systems (McArthur & Bartle 1980, Semeniuk 1990, 1995, 1997), and is the receiving basin for the Collie and Preston rivers. The estuary is bordered to the west by a barrier of quartz and calcareous sand (Quindalup Dunes) of eastward migrating parabolic dunes. The shore along the barrier consists of alternating exposed sandy promontories and more sheltered embayments, due to the staggered dune migration into the estuary, and thus exhibits a heterogeneous suite of sediments (and, potentially, habitats). The eastern shore is bordered by a low lying plain underlain by quartz sand and limestone that flanks a linear quartz sand ridge (southern extremity of the Yalgorup Plain, and the Mandurah-Eaton Ridge). This shore is more linear than the west shore, and hence is less diverse in terms of shore types. To the north, the aquatic part of the estuary is bordered by supratidal samphire flats, and to the south by the Collie and Preston river deltas. High inter-tidal salt-marsh flats fringe the aquatic part of the estuary, particularly to the north and north-west. Shallow-water platforms and slopes comprise its aquatic periphery, and an elongate muddy basin occupies its central length (Semeniuk & Meagher 1981a). The platforms are mainly of sediment derived from the flanking dunes and have been developed by wave action, and modified through erosion and deposition by currents. The northern estuary is an extensive shallow-water flat, and along the north-eastern shore is a tidal to shallow sub-tidal limestone pavement.

The southern part of the estuary has been substantially modified in the last 40 years. This has included in-filling of the original estuary outlet to the sea, redirection of the Preston River and construction of an artificial exchange channel with the ocean ("The Cut"). Construction of "The Cut" has resulted in the development of a tidal delta within the estuary, and the partial destruction of the Collie River Delta (Semeniuk & Meagher 1981a; Anon 1985b; Pen 2000).

Sedimentology

Processes which determine the modern sediment distribution within the estuary are (Semeniuk & Meagher 1981a; Semeniuk 2000):

- landward movement of barrier dunes, resulting in parabolic dunes eventually encroaching into the western shore of the estuary, providing quartz and carbonate sand to the western platform;
- reworking of dune promontories along the western shore to develop sand sheets and shoreline spits;
- incorporation of quartz sand into the estuary by wind waves eroding the eastern shore;
- wave-building and current modification of sand, forming nearshore platforms;
- transport of fluvial mud and quartzo-felspathic sand into the estuary by the Collie and Preston rivers;
- re-suspension of mud by wind waves, and subsequent transport towards low energy environments of the central basin, the northern sector of the estuary and the sheltered embayments along the west shore; and
- autochthonous accumulation of organic and calcareous mud, and calcareous sand and gravel due to aquatic and marshland flora and estuarine fauna.

Leschenault Inlet thus is filling with sediment of aeolian, fluvial and biological origin. The habitats in the estuary therefore are locally dynamic in the short term (*e.g.* five to ten years), and evolving in the long term (*e.g.* hundreds to thousands of years).

Hydrodynamics and hydrochemistry

Tides of Leschenault Inlet are diurnal and micro-tidal, with a mean spring range of 0.5 m and a maximum range of 0.9 m. The estuary is classified as a micro-tidal barrier lagoon estuary (Hayes 1975). Barometric pressure has a greater influence on water level than astronomical tides (Hodgkin & DiLollo 1958), with high pressure systems in summer contributing to low tides, and low pressure in winter producing a general rise in mean sea level (Semeniuk & Meagher 1981a). Tides in the estuary also are dampened by the restricted exchange with the ocean through "The Cut" (McComb & Lukatelich 1986). As is typical of estuaries, the waters of Leschenault Inlet commonly are turbid (Day 1981) due to resuspension of mud by wave action.

Prior to the major modifications to the south of the estuary, exchange between the estuary and the ocean took place via a 3 km-long, narrow, tidal-deltaic channel. This channel is now blocked or filled, and increased exchange with the ocean occurs through "The Cut". Fluctuations in water salinity of the estuary have stabilized, particularly to the south, by decreasing the effect of fresh water input from rivers, and by diluting with sea water the high salinity which develops with summer evaporation. Thus, the hydrodynamics, salinity fields and gradients within the estuary now are largely controlled by the interplay of a still relatively restricted exchange with the ocean, fresh water input during winter, and evaporation. Other developments that influenced hydrochemistry of the estuary include (Anon 1985b):

- the Wellington Dam, completed in 1960, which claims 2 830 km^2 of the total 3 600 km^2 of the Collie River catchment, and has reduced the flow of fresh water into the estuary;
- the Parkfield Drain, completed in 1977, which empties directly into the north of the estuary; and
- discharge of various effluents into water courses since 1983 which ultimately enter the estuary.

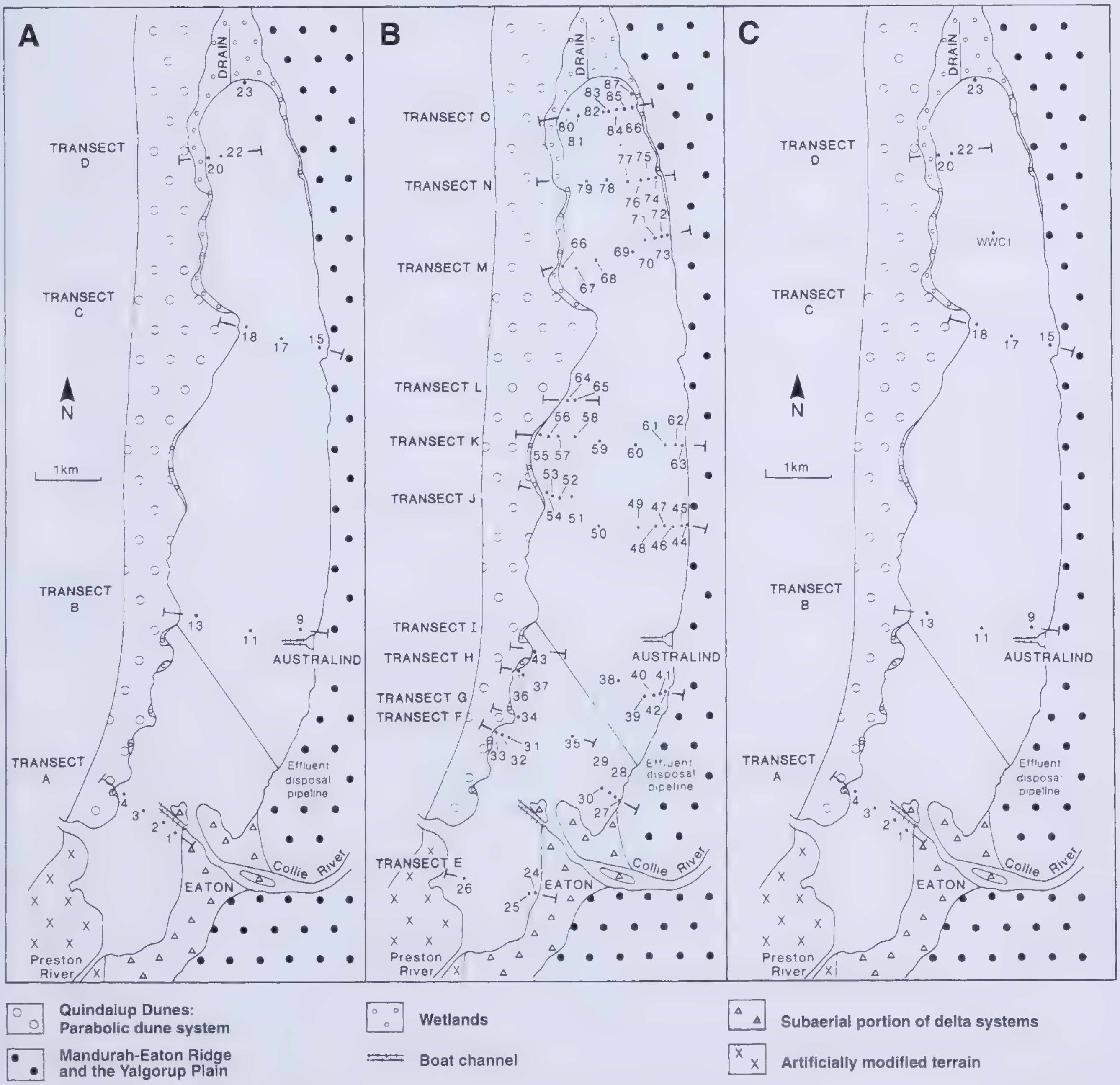

Figure 2. A: Sample sites along Transects A, B, C and D. **B:** Location of sites along Transects E to O for sampling of substrate, fauna, and flora. **C:** Water sampling sites.

Methods

This study of the physical features of Leschenault Inlet involved a range of sampling strategies, locations and times over five years between 1982 and 1987. Detritus and substrates were sampled and analysed once during this study. Macrophytes were sampled annually. During 1986/87, water quality parameters were monitored in blocks of weekly sampling during the seasonal peaks of either freshwater input during winter or evaporation during summer, separated by periods of monthly sampling. The geomorphology and bathymetry of the inlet were mapped by ground-truthing aerial photographs, and by probing the inlet floor from a boat. The study is confined to the area below the high inter-tidal to supra-tidal zone *i.e.* saltmarsh flats fringing the estuary (Semeniuk & Meagher 1981a).

A reconnaissance survey of the estuary was undertaken in February 1982 to identify the main habitat types, based on bathymetry, substrate, vegetation cover and hydrologic setting. This survey was the basis for selection of 22 sampling sites located along 4 main sampling transects oriented east-west across the estuary (Transects A-D; Table 1 and Fig 2A). Vegetation and selected physical and chemical features of habitats were monitored at these sites between 1982-1987.

A more wide-ranging survey was undertaken in December 1986 to extend the results of the 1982 survey, by quantitatively documenting bathymetry, substrates, macrophytes and fauna beyond that of the main transects (Transects E-O, Fig 2B). During this survey, substrates were sampled at the 87 sites in (Transects A-O), to determine grain size. Samples were sieved at 1 Æ intervals. The shallow stratigraphy was also determined at these sites by probing the substrate with a metal rod to 2 m. This method allowed identification of layers of mud, sandy-mud/muddy-sand, sand, shell gravel and rock.

During this survey, the presence/absence of macrophyte species was also recorded at the 87 mapping sites. Macrophytes were also quantitatively sampled annually at sites along Transects A-D, and distributions were also observed during aerial photo ground -truthing. Studies of the abundance and distribution of all species of macrophytes in the estuary have been undertaken by Lukatelich (1986) and Hillman *et al.* (2000). Macrophytes in this study are considered primarily as a component of habitat for fauna, and have only been studied from this perspective. The detritus content of the substrate was also determined at the 22 sampling sites (Transect A-D) in December 1986. Both macrophyte abundance and detritus content of the substrate were measured by collecting five replicate samples of substrate with *in situ* macrophytes, using a 25 cm x 25 cm x 25 cm box core. This sample was washed through a 1 mm mesh. Detritus and macrophytes were separated and then dried at 50 °C to a constant weight.

Table 1: Time of sampling for habitat parameters (A) water quality, and (B) other habitat variables.

A: Water quality

Data source	**Date**	**Sampling frequency**
Anon 1982-1984 (Waterways Commission of WA)	From February 1982 to May 1984	every 12 weeks
	From June 1984 to March 1987	
	June to November	every week
	December to February	every 2 weeks
	March to May	every 6 weeks
Anon 1982-1983 (State Energy Commission of WA)	December 1982 to January 1983	every 2 weeks
Anon 1982-1983 (LeProvost, Semeniuk & Chalmer, Environmental Consultants)	February 1982 to July 1983	every 6 to 8 weeks
	May 1982 to September 1982	every 1 to 2 weeks
	September 1982 to March 1983	every 6 weeks
This study	See Tables 2, 3 and 4	

B: Other habitat variables

Habitat variable	**Sampling date**
Transects A-D	
Bathymetry	December 1986
Subtrates	February 1982
Flora	February 1987
Transects E-O	
Bathymetry	December 1986
Subtrates	December 1986
Shallow stratigraphy	December 1986
Flora	December 1986

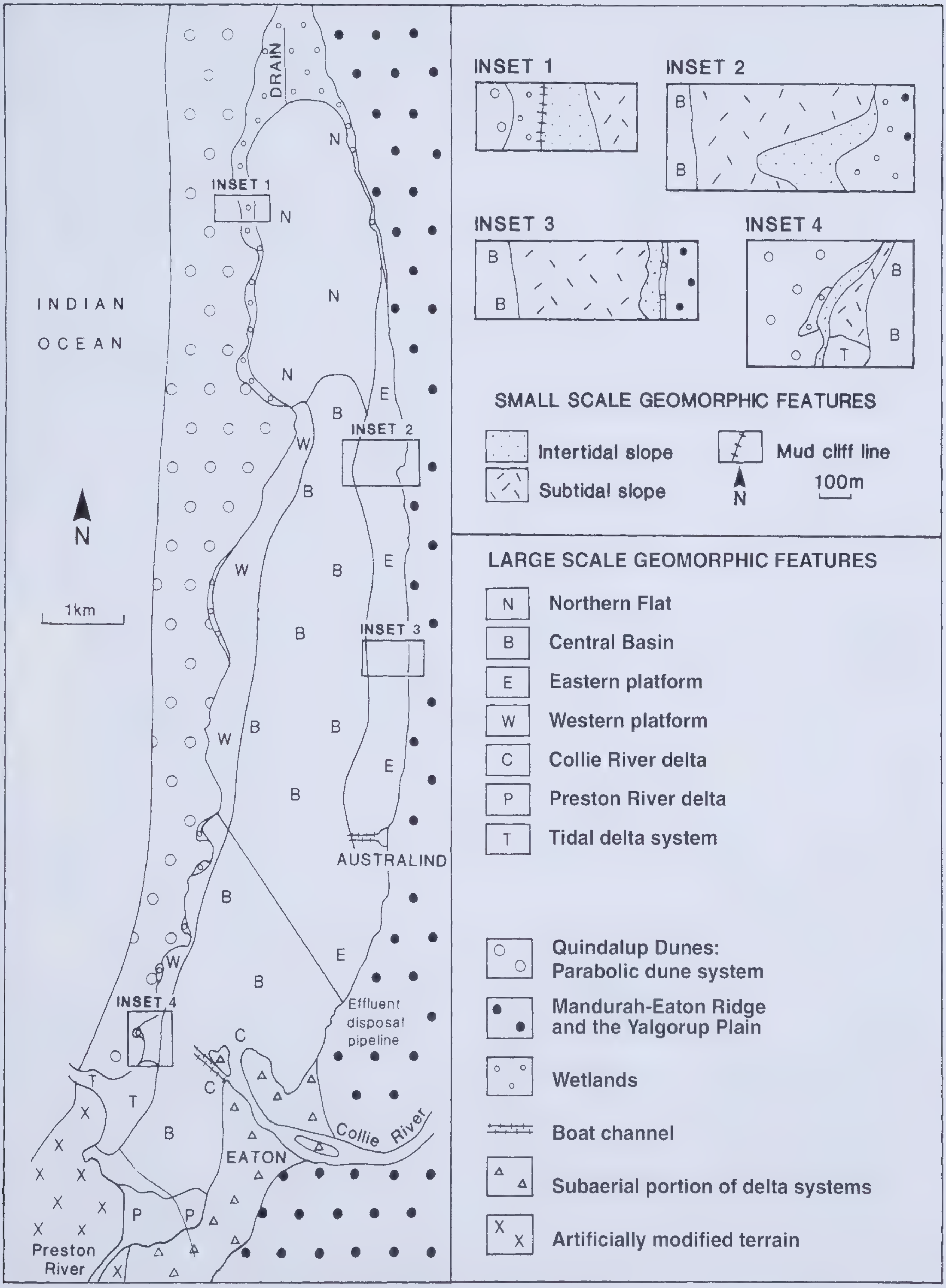

Figure 3. Map of the distribution of the large-scale geomorphic units of Leschenault Inlet.

Data on water quality were collected weekly, monthly, six-weekly and three-monthly at selected sites by Anon (1982a), Anon (1982b), Klemm, (1984, *pers comm*; information from Water & Rivers Commission)

Data collected prior to June 1986, also are considered in this study. However, these existing data were not totally adequate for this study, as the sampling programs had been designed for other objectives. Consequently, during 1986 and 1987 water salinity, temperature and oxygen concentration were sampled intensively, at selected sites along the monitoring transects (Fig 2C). These parameters were considered to be directly critical to the functions of benthos. Factors such as nitrogen and phosphorus concentration, turbidity and plant pigment concentration also can determine the water characteristics of habitats for benthic fauna, but were not included in this study. All water parameters and water samples were measured at the base of the water column, as this is the stratum directly affecting benthos. Salinity was determined using a TPS Model digital conductivity meter. Oxygen concentration initially was measured with two types of dissolved oxygen meters, a Beckman Model meter and a Hanna HI 8543 meter. Later, oxygen concentration was determined using the Winkler titration method (Riley & Chester 1971), with water samples acidified and fixed in the field to off-set plankton and detrital decay. Temperature was measured with a maximum-minimum toluene-mercury thermometer.

This study of the habitat features of Leschenault Inlet is part of a larger study that also described and monitored benthic fauna at sites used for habitat measurement and monitoring. These data are presented by Semeniuk & Wurm (2000) and Wurm (1987).

Results

Bathymetry and estuarine geomorphology

Leschenault Inlet is a long, narrow, estuarine lagoon, oriented north-south, approximately 13 km long and 1.5 km to 2.5 km wide. The estuary can be divided into five bathymetric and geomorphic units: central basin, northern flat, western platform, eastern platform, and the delta systems (Fig 3).

The central basin is approximately 10 km by 1 km, and has an average depth of 1.75 m, reaching a maximum of 2.5m. The bathymetrically deepest part is adjacent to the eastern platform. The contact between the basin and the eastern platform is abrupt, while along its western edge the basin slopes more gently into the western platform. The basin surface is very gently undulating to flat, and marked by centimeter-sized burrows.

The northern flat occupies the northern quarter of the estuary. An inter-tidal slope, approximately 200 m to 500 m wide, flanks the sub-tidal, central area of the flat, which has a maximum depth of approximately 50 cm. The inter-tidal surface has shallow, metre-sized depressions and channels that remain water-filled during low tides. The inter-tidal zone adjoins a low (10-30 cm) mud cliff at the edge of fringing marshlands. A limestone pavement appears locally in north-eastern parts of the flat, and meets a low cliff cut into limestone at the shoreline.

The eastern platform is approximately 500 m wide and slopes gently from the estuary shore to a steep contact with the basin at depths of approximately 1 m. Along the shore there is an inter-tidal slope of variable width but up to approximately 100 m wide, which is frequently exposed during periods of low water in summer. In front of the flanking marshlands, this platform adjoins low (10-20 cm) mud cliffs or very narrow beaches. The platform surface is hummocky to irregular due to wave scouring at the metre scale (Semeniuk & Meagher 1981a), and burrowing by crabs, fish and worms at the decimeter scale. The littoral zone is marked by cuspate shores, most probably developed by wind waves acting on the platform and sandy shore.

The western platform, approximately 200 m to 400 m wide, slopes gently from shore towards its contact with the central basin, where the water depth is approximately 1 m. It consists mostly of a gently inclined platform that laterally grades to a more inclined slope or ramp, depending on its disposition relative to adjoining, encroaching dunes. Its surface is marked by burrows and shallow metre-sized depressions, particularly in depths < 30 cm. An inter-tidal slope occurs as an irregular narrow (*ca* 50 m) zone which adjoins either narrow sandy beaches (where the shore is an encroaching dune) or low (10-20 cm) cliffs cut into mud (where the shore is salt marsh).

The Collie River delta protrudes from the shore as a subaerial and aquatic lobe in the south of the estuary. The delta has components of delta front sand, subaerial delta marshes, beach ridges and cheniers, abandoned channels, levees, distributary channels, and mid-channel islands. At its western edge the delta abuts the central basin relatively sharply, but grades more gently onto the eastern platform at its northern edge. Much of the delta front is inter-tidal, and it grades down to a maximum depth of 40 cm at its basin edge. The Preston River delta complex occurs in the extreme south of the estuary, and a dynamic tidal delta system has developed at the mouth of "The Cut". These latter two systems are not discussed further in this study.

Surface Substrate Types and Distribution

The type and distribution of substrates are significant in determining the distribution of the benthic fauna (Yonge 1976). For example, the distribution of deposit feeders can be largely determined by particle size, due to their feeding mechanisms (Tunnicliffe & Risk 1977). The predominant substrates in the Inlet, in order of increasing surface area, are mud, sand, muddy-sand and sandy-mud. The distribution of three most wide-spread sediment grain sizes (coarse sand, medium sand, and mud) are shown in Fig 4. Granulometry of sediments collected from the sampling sites along Transects A-D are shown in Figs 5-8. Diagrams for Transects E-O are presented by Wurm (1987), or are available from the authors. The estuary is underlain predominantly by mud in the central and northern sectors, sand and muddy-sand along the eastern platform, mud, muddy-sand, sandy-mud and sand along the western platform, and predominantly sand around the delta systems.

The central basin is underlain by muddy sediment

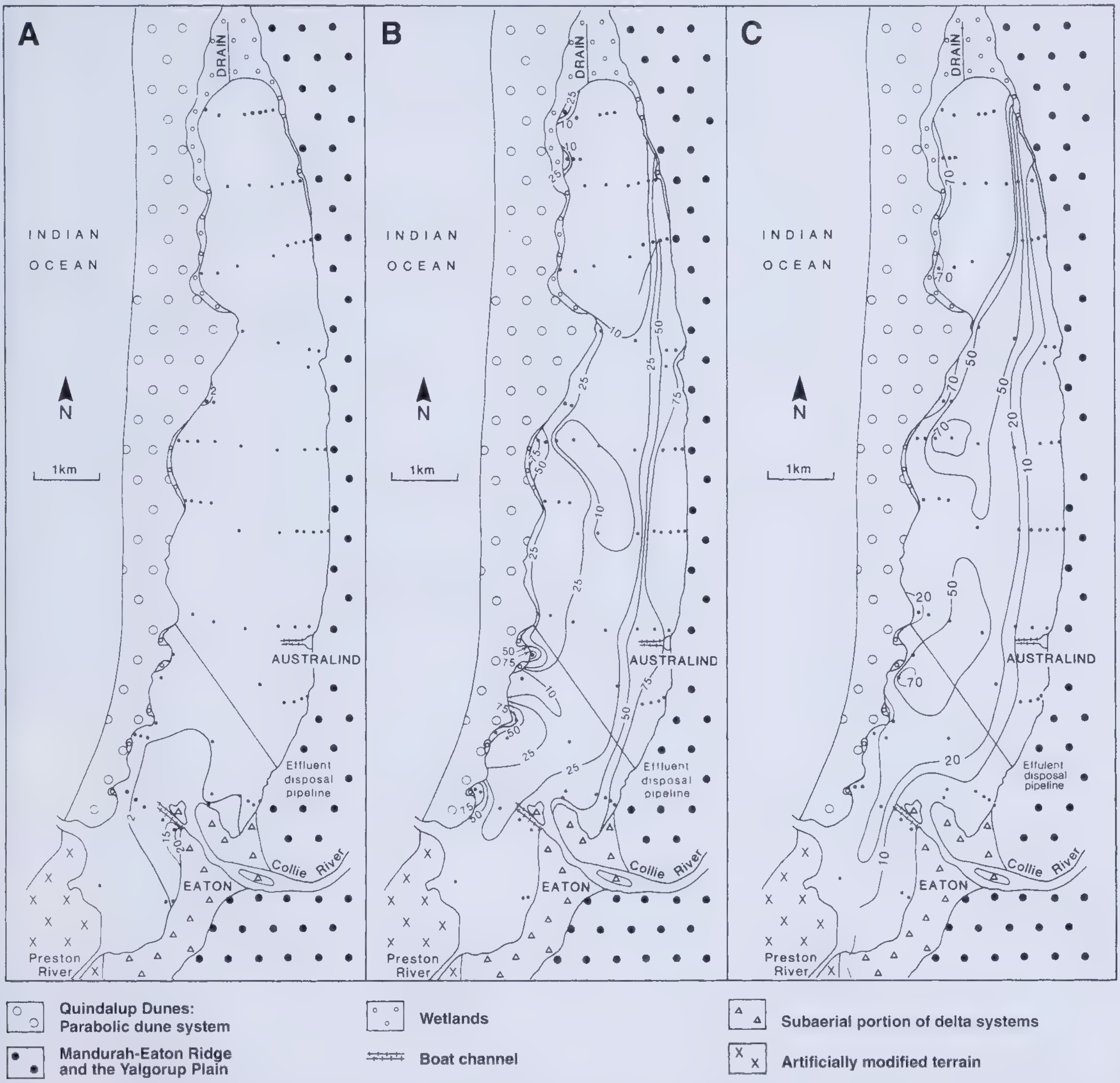
A
B
C
INDIAN OCEAN
N
1km
DRAIN
AUSTRALIND
Effluent disposal pipeline
EATON
Collie River
Preston River
10
25
50
75
20
70
Quindalup Dunes: Parabolic dune system
Mandurah-Eaton Ridge and the Yalgorup Plain
Wetlands
Boat channel
Subaerial portion of delta systems
Artificially modified terrain

Figure 4. Contour maps of percentage content of selected grain sizes of substrates in Leschenault Inlet estuary. Dots indicate points from which substrate samples were collected. **A:** Distribution of coarse sand (> 500 mm - 1 mm particle diameter). **B:** Distribution of medium sand (>250 mm - 500 mm particle diameter). **C:** Distribution of mud (< 63 mm particle diameter).

(Figs 4B, 7, 8). Distribution of sediment types indicates that there has been local influx of sand from the reworking and incorporation of sand on flanking platforms (*e.g.* Fig 7, sites 10 and 13). Sandy-mud also occurs locally (*e.g.* Fig 5, site 3), where the sand fraction was primarily shell fragments, unlike the sand of the deltas and platforms, which was mainly quartz. The northern flat is underlain by muddy sediments (generally > 70% mud). However sand from the eastern platform extends into the muds of the northern flat along its eastern shore (Fig 4C; Fig 9F). Similarly, the patterns of heterogeneity along the western platform shore also are evident along the western shore of the northern flat (Fig 4B,C).

The eastern platform is underlain mainly by medium sand with < 10% mud (Fig 4B,C). Sand texture along the length of the eastern platform is relatively homogeneous, with an increase in mud content towards the central basin. This relative homogeneity reflects the origin of the platform (*i.e.* the reworking of a linear, sandy shore). The western platform substrates are more texturally heterogeneous, similarly reflecting their origin (*i.e.* the staggered encroachment of dunes into the estuary) (Fig 4B,C). At the tip of dune promontories sand sheets have developed as dunes are reworked at the shore. Distribution of substrate types indicates that muddy-sand and sandy-mud substrates develop over time as mud is mixed into what was formerly dune sand.

The Collie River delta system is underlain mainly by medium and coarse angular quartz and felspar sand, with some very coarse sand and granules (Figs 4A, Fig 5, 6). The northern edge of the delta lobe is underlain by mainly

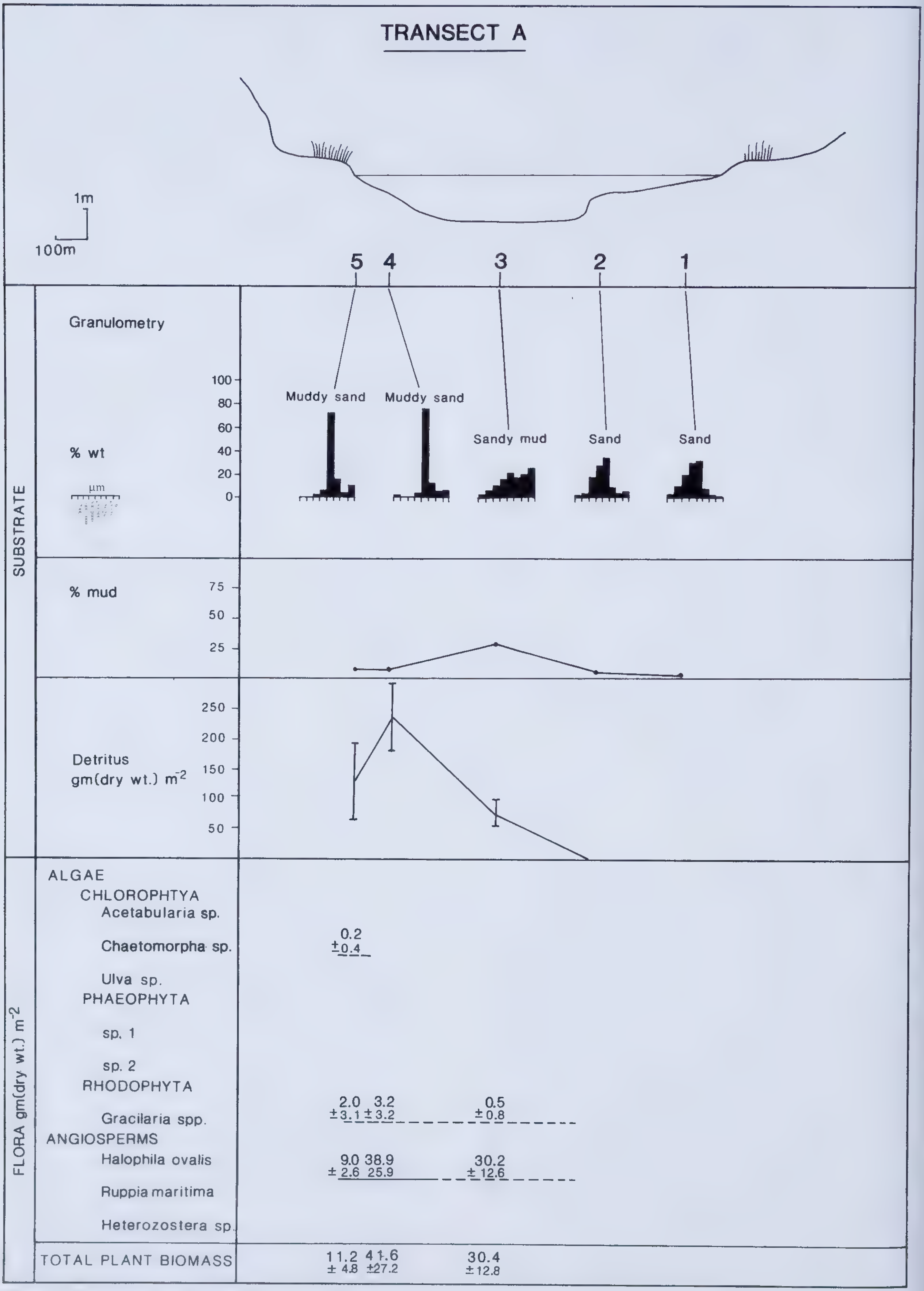

Figure 5. Geomorphic profile across Leschenault Inlet, showing substrate and macrophyte characteristics of sites along Transect A. Location of site is shown in Fig 2A.

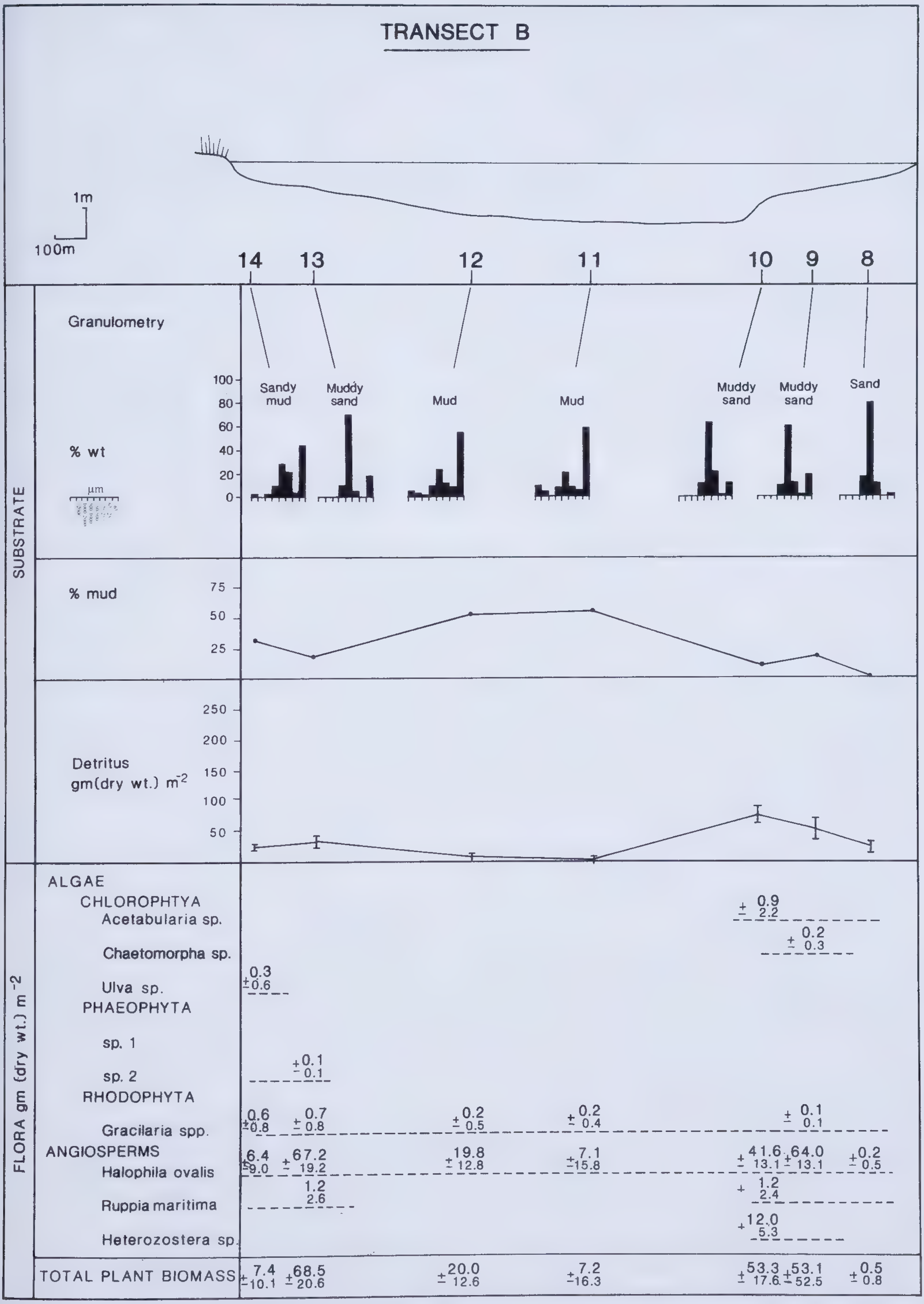

Figure 6. Geomorphic profile across Leschenault Inlet, showing substrate and macrophyte characteristics of sites along Transect B. Location of site is shown in Fig 2A.

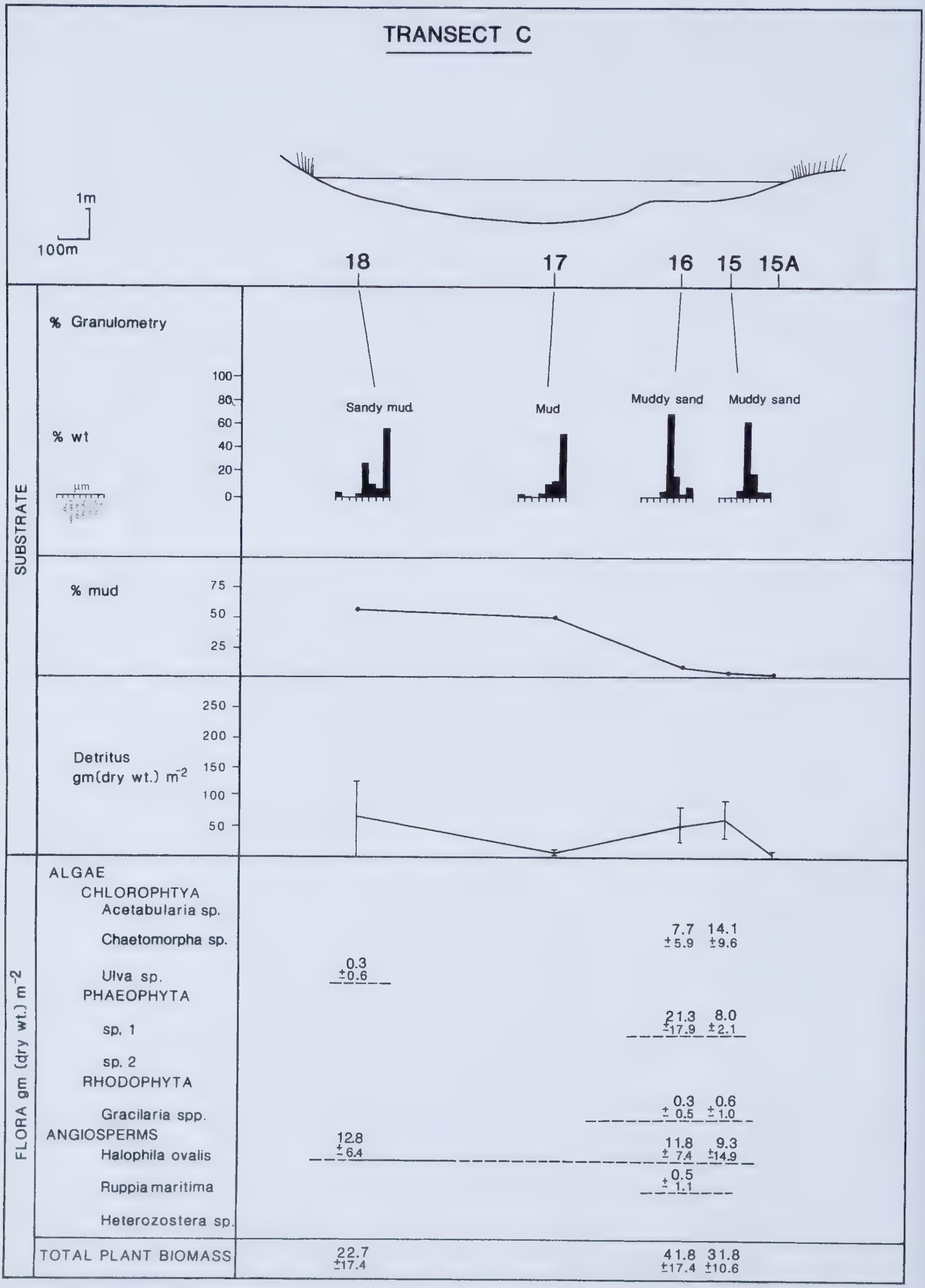

Figure 7. Geomorphic profile across Leschenault Inlet, showing substrate and macrophyte characteristics of sites along Transect C. Location of site is shown in Fig 2A.

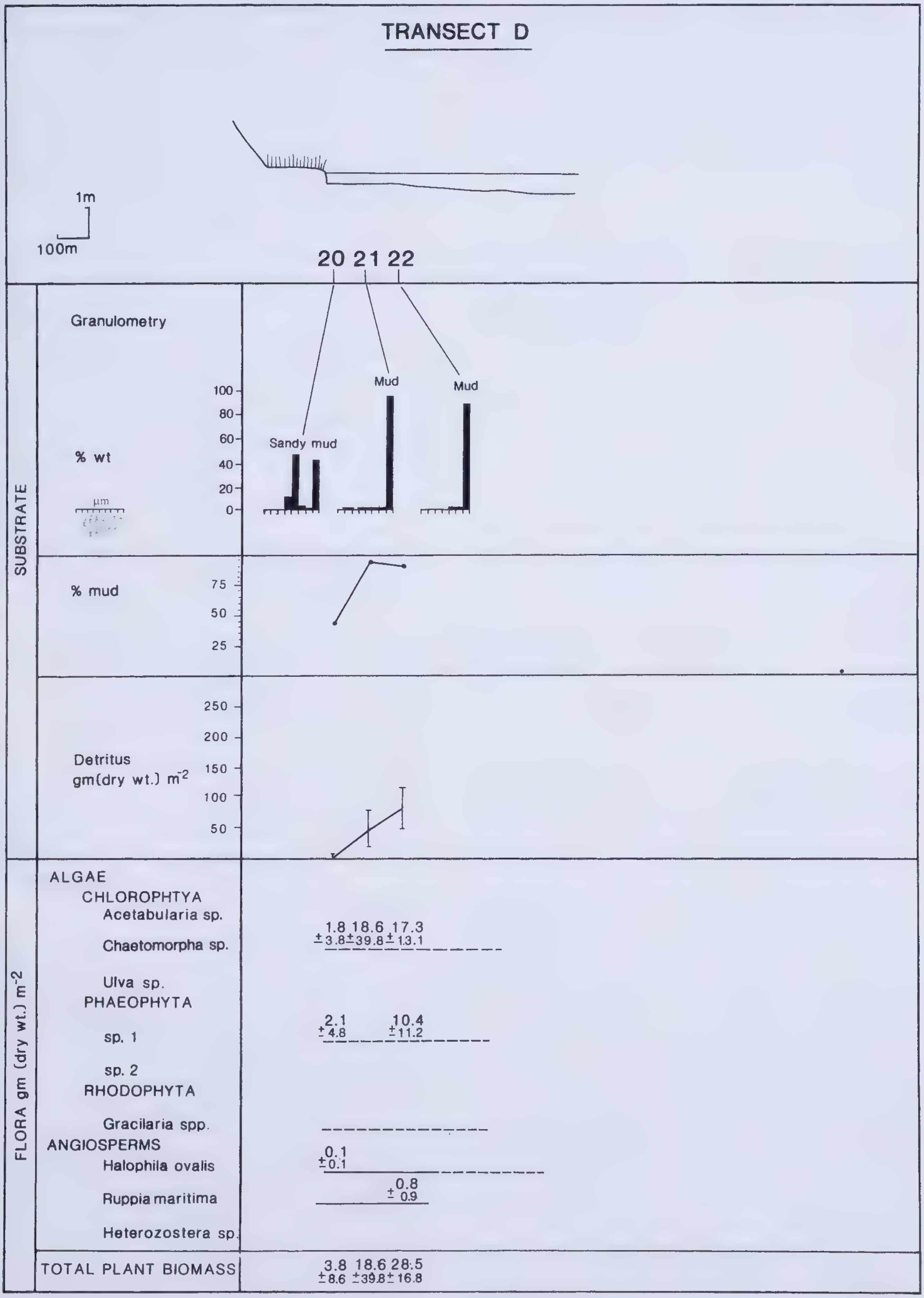

Figure 8. Geomorphic profile across Leschenault Inlet, showing substrate and macrophyte characteristics of sites along Transect D. Location of site is shown in Fig 2A.

medium sand with less coarse sand and little very coarse sand, probably due to the lower energy regime there. The delta is a dynamic system due to the continuing deposition of sediment by the Collie River and reworking of the delta at its seaward edge. For example, during this 5-year study, a 10 cm thick sheet of coarse sand encroached over south-western sites on the delta, and a 50 cm thick sheet of medium sand encroached over western and northern sampling sites on the delta.

Detritus occurs most abundantly in the substrates of the eastern and western platforms, where macrophytes are also most abundant (Figs 5-8). However, despite relatively minor macrophyte cover across the northern flat, the detritus content here also is relatively high (Figure 8). This may be due to drifts of floating algae washed in from marine sources (informally observed during the course of this study), and input from the marshes fringing its shore. Detritus is low in muds of the central basin, in unvegetated sands of the delta, and inter-tidal slopes of the eastern platform (Figs 5-8). Note, however that detritus was sampled only once during this study. It is likely that this substrate character may vary with seasonal variations in macrophytes.

Shallow stratigraphy

The shallow stratigraphy provides information on the homogeneity of substrata with depth, and the extent of interlayering of sediment types due to burial of previous substrates. This in turn provides information on the origin and development of substrate types, and an indication of the evolution and dynamics of habitats and associated biota. Shallow stratigraphy also influences deep burrowing fauna and rooted vegetation. Information on shallow stratigraphy is also presented in Semeniuk & Meagher (1981a), Wurm (1987) and Semeniuk (2000).

The northern flat is generally underlain by homogeneous mud, though a more complex stratigraphy occurs along its north-eastern shore indicating dynamic short-term habitat variations (Fig 9 Transects J, K). Limestone also crops out at the north-north-eastern shore and forms an undulating surface, periodically buried under a thin cover of mud and interlayered muddy and sandy sediment. The muddy-sand and sand substrates of the eastern platform and the mud of the central basin are homogeneous at depth, indicating relative long-term stability in habitats (Fig 9 Transect F sites 44-48, Fig 9 Transect G sites 61-63). The western platform, in contrast, has a complex shallow stratigraphy indicating a dynamic environment: dune encroachment alternating with mud deposition has resulted in the interlayering of muddy-sand, mud, and sandy-mud at shallow depths (Fig 9 Transect F sites 51-54). Mud also accumulates in the more protected environments between sand promontories (Fig 9 Transect B, sites 31-33, Fig 9 Transect H, sites 36-37). Interlayering of muddy-sand and sandy-mud also occurs in the delta system due to alluvial input from the rivers and the constant wave reworking of the delta front (Fig 9 Transect E).

Water chemistry

Data on salinity, oxygen and temperature of estuarine water between 1982 and 1986 from Anon (1982a) and Anon (1982b) sampled in localities close to sites in the central basin of this study are presented in Tables 2-4 and Fig 10. Data for sites other than those in the central basin are not available prior to 1986. Data on water sampled during this study are presented in Fig 11.

The extremes of hydrochemistry may be more significant in determining the long term distribution of biota, than are the mean conditions prevailing in a given habitat. Ranges of values for water parameters, as well as means, at each sampling site are presented in Table 5. These data form the basis for the identification of categories of water types in the estuary.

Salinity. Waters along the length of the estuary are poikilosaline *i.e.* undergo fluctuating salinity (Table 2; Figs 10 & 11). Patterns of variation indicate that salinity changes both within and between years (Fig 10). For example, at site A3 in the lower estuary, there was a marked drop in salinity in 1983. This was not recorded again at this site during subsequent years of monitoring. However, at sites C17 and D23, located in the mid and upper estuary respectively, a similar decrease in salinity was recorded in each subsequent year of monitoring. This may reflect the damping effect on salinity, due to the input of sea water through "The Cut". This influence does not appear to extend to the north of the estuary during the times of maximum freshwater input (winter).

In the north, salinity varies from hyposaline to hypersaline throughout the year (salinity terms after Hammer 1986). For example, during the 1986-1987 study period, water salinity in the north of the estuary (Transect D sites 20 and 21) varied from 21 - 62 ‰ (Table 2). In the mid estuary, salinity fluctuated within a range of mesosaline values. For example, on Transect B at site 9, salinity varied between 23.5 - 45.0 ‰ (Table 2). At the Collie River delta, salinity varies from hyposaline to mesosaline. For example, during the 1986-1987 study period, salinity varied from 4.7 - 42.5 ‰ (Table 2, Transect A site 3).

The north-south differences in fluctuation patterns are illustrated in a plot of water salinity at sites along the north-south axes of the central basin and western platform (Fig 12). This graph illustrates a more stable, year-round salinity to the south of the estuary (sites A3, A4), a more variable salinity in the middle of the estuary (*e.g.* sites C17 and C15) and the most variable salinity in the northern end of the estuary.

Oxygen. Estuary waters are generally well oxygenated throughout the year. Dissolved oxygen concentrations even in summer are generally > 5 mg L^{-1}. Highest oxygen concentrations were recorded at well-vegetated sites in shallow water. Even though the solubility of oxygen decreases with temperature (Gross 1972), high oxygen concentrations frequently occurred with high water temperature at shallow sites. This is possibly due to increased plant metabolism under warm conditions, resulting in greater oxygen release into the water (bubbles of oxygen were observed adhering to vegetation during some surveys). Overall, there was no clear correlation between variation of oxygen concentration and other water parameters, and oxygen concentration in the estuary appeared to vary independently of temperature and salinity (Figs 9 & 10).

Temperature. The temperature of a relatively shallow water body, such as Leschenault Inlet, is typically determined

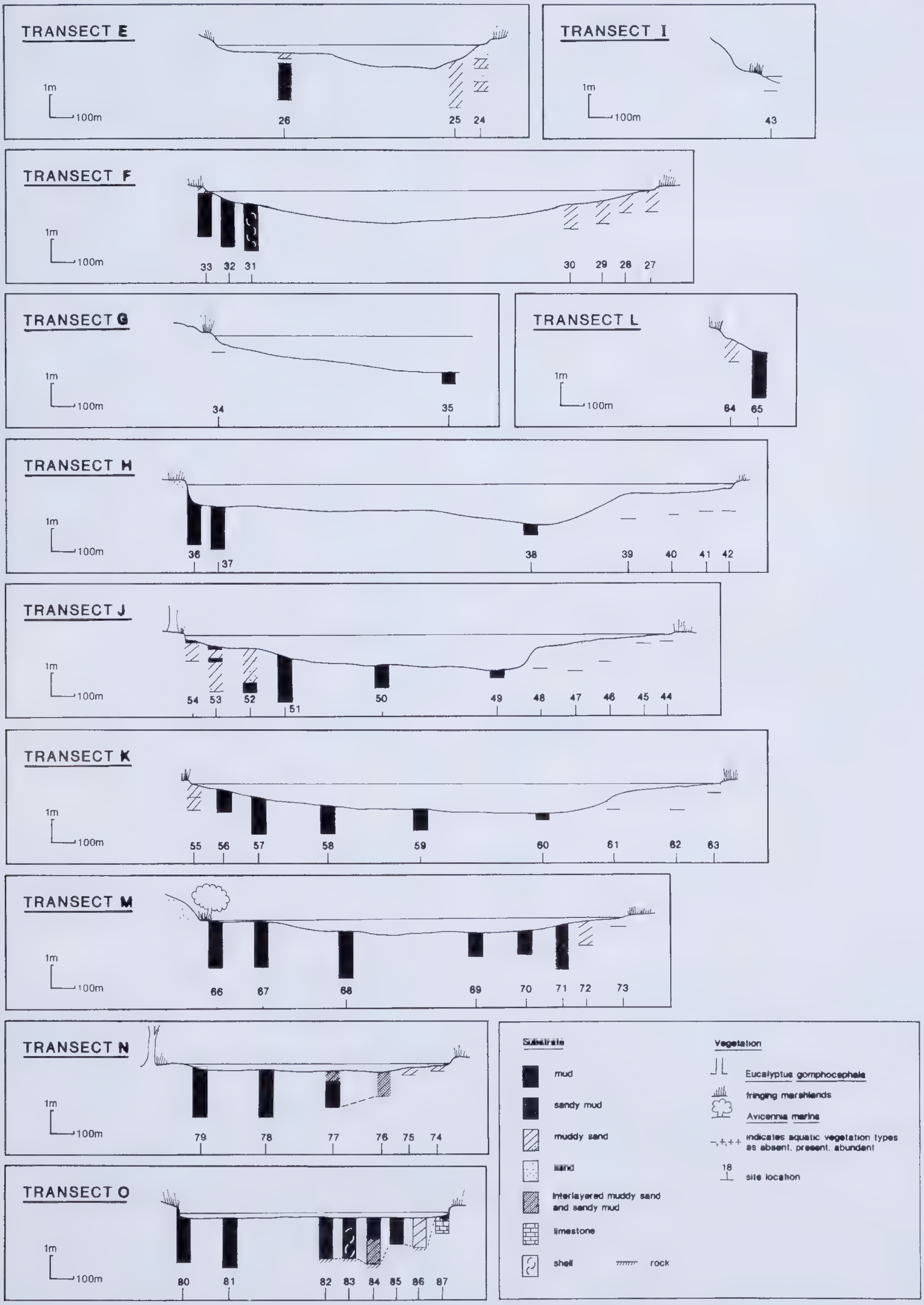

Figure 9. Shallow stratigraphy at sites along Transects E-O. Location of sites is shown in Fig 2.

Table 2. Water salinity (‰) recorded in Leschenault Inlet at sites along Transects A-D during this study.

SITE		TRANSECT A							TRANSECT B							TRANSECT C					TRANSECT D			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Week 1	5/10/1986	24.0	31.0	34.0	35.0	35.0	24.0	25.0	32.0	33.5	33.5	33.5	33.5	32.5	32.5	29.5	30.5	29.5	30.0	30.0	28.5	29.0	30.0	ns
Week 2	14/10/1986	27.0	33.5	35.5	34.0	35.0	34.5	32.5	33.5	33.5	33.5	33.5	33.5	34.0	33.5	31.0	30.0	30.5	31.5	32.0	31.0	30.0	31.0	3.5
Week 3	21/10/1986	ex	15.0	33.5	32.0	ex	ex	ex	ex	32.5	33.5	34.0	29.5	32.0	ex	34.0	32.0	ex	32.0	33.5	35.5	ns	34.5	315.0
Week 4	29/10/1986	17.5	33.0	35.5	34.5	34.5	32.0	21.5	34.5	34.5	34.5	34.5	34.5	34.0	35.0	34.0	34.0	33.5	33.0	33.0	35.0	35.0	35.0	4.5
Week 5	4/11/1986	ex	21.0	35.5	36.0	36.5	ex	ex	35.5	35.5	35.5	35.5	35.5	35.5	36.0	36.0	36.0	ex	35.5	35.5	35.5	35.5	36.0	ns
Week 6	13/11/1986	31.5	35.0	37.0	37.0	36.5	29.5	29.5	36.5	36.0	36.0	36.0	36.0	36.5	36.0	36.0	36.5	37.0	36.0	36.0	36.5	36.5	36.5	235.0
Week 7	20/11/1986	33.5	35.0	36.0	36.0	36.5	ex	ex	36.0	36.0	36.0	36.0	36.0	36.0	36.5	37.0	37.0	38.0	36.5	36.5	41.5	35.0	39.0	440.0
Week 8	27/11/1986	41.5	39.5	42.5	43.5	41.5	ex	ex	45.5	45.0	44.5	44.5	44.5	46.0	45.5	48.5	47.0	48.0	46.0	47.0	53.0	53.0	52.0	ns
Week 9	2/12/1986	17.5	32.5	34.0	35.5	36.0	ex	ex	36.0	36.0	36.0	36.5	35.5	36.0	36.0	37.0	37.0	40.5	39.0	37.0	45.0	44.0	43.0	5.0
Week 13	26/12/1986	36.5	36.0	34.5	36.0	ns	ns	ns	37.0	37.0	37.0	ns	38.0	35.0	36.5	39.0	42.5	ns	46.0	36.5	47.5	48.0	47.5	115.0
Week 17	29/01/1987	ns	36.0	37.0	38.0	ns	ns	ns	ns	43.0	ns	44.0	ns	ns	ns	47.5	ns	ns	46.0	ns	62.0	ns	62.0	350.0
Week 18	5/02/1987	36.0	36.5	37.0	36.5	ns	ns	ns	ns	41.5	ns	38.5	ns	37.0	ns	44.0	ns	ns	42.5	39.5	53.0	ns	53.0	465.0
Week 19	12/02/1987	32.5	35.0	36.0	35.5	ns	ns	ns	ns	38.0	ns	38.0	ns	36.5	ns	43.0	ns	ns	42.5	41.0	59.0	ns	56.0	575.0
Week 20	19/02/1987	36.5	36.0	36.0	36.0	ns	ns	ns	ns	39.5	ns	39.5	ns	36.5	ns	45.5	ns	ns	41.5	41.0	50.0	ns	50.5	595.0
Week 21	25/2/87	36.0	36.0	37.5	38.5	ns	ns	ns	ns	42.0	ns	39.8	ns	39.0	ns	48.0	ns	ns	45.0	44.0	53.0	ns	52.0	535.0
Week 23	9/3/87	35.5	36.1	36.5	36.5	ns	ns	ns	ns	39.5	ns	37.5	ns	38.0	ns	44.5	ns	ns	42.0	43.5	56.0	ns	52.0	ns
Week 27	30/03/1987	35.5	36.0	36.0	36.0	ns	ns	ns	ns	39.5	ns	36.0	ns	37.5	ns	43.5	ns	ns	39.0	41.5	47.0	ns	46.0	480.0

Footnotes: 1. "ex" indicates that a site was exposed at that time. 2. "ns" indicates that a site was not sampled at that time.

Table 3. Oxygen concentrations (mg.1.-1) recorded at all sites during the water quality monitoring programme.

SITE		TRANSECT A							TRANSECT B							TRANSECT C					TRANSECT D		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Week 1	5/10/1986	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Week 2	14/10/1986	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Week 3	21/10/1986	ex	10.2	8.5	7.0	ex	ex	ex	ex	10.0	9.0	9.3	8.3	7.0	ex	10.8	12.3	12.5	19.0	ex	7.8	ns	8.0
Week 4	29/10/1986	9.3	8.4	9.4	9.1	8.7	11.9	9.7	8.7	8.3	8.5	8.2	9.0	8.8	10.6	10.1	10.9	9.3	17.0	10.7	9.2	9.4	9.0
Week 5	4/11/1986	ex	6.0	6.0	6.3	11.6	ex	ex	10.5	9.8	6.8	5.7	5.9	8.0	11.6	12.9	11.0	9.8	15.5	ex	8.3	8.3	10.6
Week 6	13/11/1986	11.2	11.0	11.0	12.1	12.5	12.0	13.8	9.1	8.8	9.9	9.6	9.0	10.0	10.5	9.8	9.8	9.9	10.5	10.3	ns	ns	ns
Week 7	20/11/1986	ns	ns	ns	ns	ns	ns	ns	12.8	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	10.5	12.5	13.5
Week 8	27/11/1986	9.9	9.9	9.8	8.5	10.9	ex	ex	14.5	12.6	9.7	10.8	10.2	11.1	14.8	15.0	11.3	11.0	16.5	11.9	11.2	13.3	14.6
Week 9	2/12/1986	14.2	10.2	10.0	10.1	13.3	ex	ex	15.3	12.1	9.5	9.9	10.1	9.9	11.8	19.0	14.8	10.1	19.3	10.6	8.5	8.9	9.5
Week 13	26/12/1986	11.8	10.1		9.3	11.8	ex	ex	10.6	7.0	11.6	ns	9.6	11.8	11.8	11.8	11.8	7.2	11.7	ex	ns	ns	ns
Week 17	29/01/1987	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Week 18	5/02/1987	7.6	7.3	6.5	6.2	ns	ns	ns	ns	20.0	ns	6.2	ns	8.8	ns	11.0	ns	10	20.0	ns	11.8	ns	10.5
Week 19	12/02/1987	10.9	10.8	10.0	12.2	ns	ns	ns	ns	11.0	ns	9.3	ns	8.1	ns	13.5	ns	8.5	12.0	ns	16.2	ns	16.6
Week 20	19/02/1987	8.0	7.2	7.0	6.7	ns	ns	ns	ns	9.3	ns	7.4	ns	10.2	ns	9.6	ns	6.9	12.0	ns	8.5	ns	9.6
Week 21	25/2/87	8.2	7.7	7.0	7.7	ns	ns	ns	ns	12.2	ns	7.7	ns	11.5	ns	9.4	ns	8.5	12.5	ns	6.6	ns	6.7
Week 23	9/3/87	8.0	8.5	7.7	7.7	ns	ns	ns	ns	9.3	ns	8.0	ns	9.8	ns	9.8	ns	8.3	10.7	ns	9.0	ns	9.1
Week 27	30/03/1987	8.2	8.3	8.0	8.0	ns	ns	ns	ns	8.5	ns	7.5	ns	8.2	ns	9.9	ns	8.5	11.1	ns	7.2	ns	7.5

Footnotes: 1. "ex" indicates that a site was exposed at that time. 2. "ns" indicates that a site was not sampled at that time.

Table 4. Water temperature (degrees °C) recorded in Leschenault Inlet at sites along Transects A-D during this study.

SITE		TRANSECT A							TRANSECT B							TRANSECT C					TRANSECT D		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Week 1	5/10/1986	17.0	17.0	17.5	18.0	19.5	24.0	20.0	17.5	17.5	18.3	18.5	16.9	18.8	19.8	18.0	17.5	17.0	20.5	19.5	17.5	17.5	17.0
Week 2	14/10/1986	17.0	17.0	15.0	16.5	16.5	17.5	15.5	16.5	16.5	16.5	16.0	16.0	17.0	17.0	17.5	17.5	17.0	17.0	16.5	17.0	17.5	17.0
Week 3	21/10/1986	ex	20.0	18.0	18.5	ex	ex	ex	ex	20.5	18.5	18.5	17.5	21.0	ex	22.0	20.0	20.0	20.5	ex	21.5	ns	21.5
Week 4	29/10/1986	17.5	17.0	17.0	17.5	20.0	23.5	21.5	19.5	19.5	18.8	20.0	19.5	17.8	19.5	21.5	20.0	20.0	19.0	19.5	19.0	20.5	20.5
Week 5	4/11/1986	ex	21.5	18.5	19.0	ex	ex	ex	22.5	21.0	20.5	20.5	20.5	21.0	27.0	24.0	23.5	21.5	25.5	ex	18.0	15.0	19.0
Week 6	13/11/1986	19.5	20.5	20.0	20.0	20.0	23.0	23.0	21.5	21.5	21.5	21.5	21.0	22.0	22.5	23.0	22.0	22.5	23.0	22.5	24.5	24.0	23.4
Week 7	20/11/1986	29.5	24.5	24.0	24.5	28.5	ex	ex	30.0	27.0	24.5	25.0	25.5	29.5	33.0	31.0	31.0	27.5	32.0	29.5	27.5	27.5	27.5
Week 8	27/11/1986	23.5	22.0	21.5	22.0	23.0	ex	ex	26.5	24.5	21.5	21.5	21.5	25.0	28.0	27.0	26.0	22.0	27.5	24.0	30.0	29.0	2*9
Week 9	2/12/1986	23.5	21.0	21.0	22.0	22.5	ex	ex	24.0	22.0	20.5	21.0	21.0	23.0	31.0	26.0	24.0	21.5	27.0	29.0	24.0	25.0	26.0
Week 13	26/12/1986	30.0	27.0	ns	23.5	23	ex	ex	18.5	24.0	24.0	ns	24.5	26.0	29.0	26.5	27.0	22	27.0	ns	30.0	32.0	31.0
Week 17	29/01/1987	ns	26.5	24.0	22.0	ns	ns	ns	ns	24.0	ns	22.5	ns	ns	ns	29.0	ns	24.0	ns	ns	24.5	ns	23.0
Week 18	5/02/1987	25.0	25.0	22.5	23.0	ns	ns	ns	ns	26.0	ns	24.0	ns	26.0	ns	28.5	ns	25	28.5	ns	30.0	ns	30.0
Week 19	12/02/1987	25.5	24.5	22.0	22.5	ns	ns	ns	ns	27.0	ns	23.0	ns	25.0	ns	31.5	ns	24	31.0	ns	26.5	ns	26.0
Week 20	19/02/1987	20.5	19.5	21.5	20.5	ns	ns	ns	ns	21.5	ns	20.5	ns	20.5	ns	22.5	ns	21	22.5	ns	19.5	ns	20.0
Week 21	25/2/87	22.5	22.0	20.5	21.0	ns	ns	ns	ns	24.0	ns	21.5	ns	23.5	ns	26.5	ns	22	27.0	ns	19.0	ns	20.5
Week 23	9/3/87	22.0	22.5	22.0	22.5	ns	ns	ns	ns	24.0	ns	23.0	ns	23.0	ns	23.5	ns	23	23.0	ns	22.0	ns	21.0
Week 27	30/03/1987	21.0	21.0	21.0	21.0	ns	ns	ns	ns	21.0	ns	20.5	ns	22.0	ns	21.0	ns	20.5	22.0	ns	19.0	ns	19.0

Footnotes: 1. "ex" indicates that a site was exposed at that time. 2. "ns" indicates that a site was not sampled at that time.

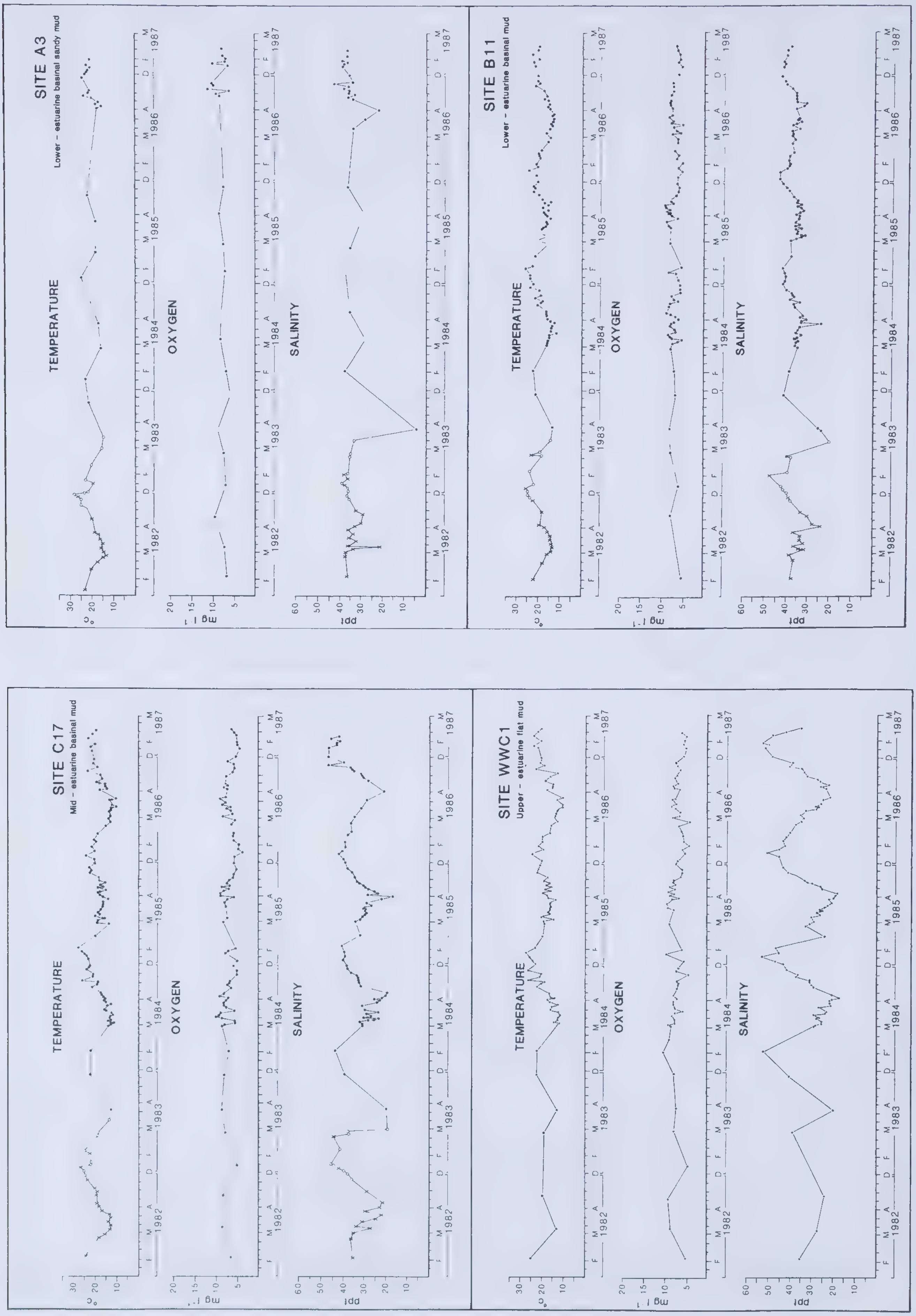

Figure 10. Water quality data for selected sites collected (Anon 1982a, b; Anon 1985b; Klemm 1984)

by air temperature and wind. Winter temperatures in deep water were frequently below 15 °C, while summer temperatures are frequently at or above 25 °C, but typically around 22 °C (Table 4 & Fig 10). The deep water of the central basin has a temperature range of approximately 10 °C, and maintains a generally lower temperature than shallower sites. Shallower water sites, located on eastern and western platforms, Collie delta and the northern flat have winter water temperatures of approximately 15 °C, and summer temperatures of approximately 30 °C. Shallow water sites, with dark muddy substrates (*e.g.* D20, D21, D22, C18 and B14) experienced the highest temperatures. A temperature of 32 °C was recorded in one shallow pool on the northern flat during the 1986 survey (fine, dark mud absorbs more solar radiation than lighter coloured and coarser grained sandy substrates; see Hasse & Dobson 1986, p15). It also was observed in the field that muddy substrates become heated to a depth of at least 10 cm during summer.

Distribution of Macrophytes

A total of 3 species of seagrass and at least 7 species of algae were recorded in the Leschenault Inlet estuary during this study. The seagrass species were *Halophila ovalis*, *Ruppia megacarpa* and *Heterozostera tasmanica*. Algae species were *Chaetomorpha* sp, *Gracilaria* spp., *Ulva* sp, *Acetabularia* sp and two species of Phaeophyta (including *Hormophysa triquetta; cf* Hillman *et al.* 2000). *Halophila ovalis* is the most widespread species of seagrass in the estuary, and contributes the greatest biomass to the macrophytes.

Turbidity limits seagrass distribution (McComb *et al.* 1981), and in Leschenault Inlet at depths > 1.5 m seagrass is restricted and patchy in distribution (Fig 5-8; data for survey transects is available in Wurm 1987 or from the authors).

The greatest biomass of macrophytes generally occurred on mud, sandy-mud and muddy-sand of the western platform, where *Halophila ovalis* dominated (*e.g.* Fig 5 sites 4; Fig 7 site 13). *Gracilaria* spp. also occurred more commonly in the south of the estuary. *Ruppia megacarpa* occurred occasionally, and mainly in shallow inter-tidal depressions that retain water at low tide. Some *Chaetomorpha* and *Gracilaria* also occurred in these pools. Minor occurrences of *Ulva* sp were noted, and *Heterozostera tasmanica* occurred on sandy substrates at the tip of encroaching dunes.

Sandy substrates of the eastern platform supported a relatively dense cover of *Halophila ovalis* (*e.g.* Fig 7 sites 9, 10). A sparse cover of *Ruppia megacarpa* typically occurred at the more sandy shoreward edge of the platform in a few centimetres of water but also extended into the *Halophila* zone (*e.g.* Fig 7, site 9). *Gracilaria* spp also occurred in the *Halophila* zone. *Heterozostera tasmanica* was recorded in the mid estuary zone of the platform (*e.g.* Fig 7 sites 8,9,10). Toward the north of the eastern platform, *Chaetomorpha* and a phaeophyte species became more common (*e.g.* Fig 8 sites 15,16).

Sandy substrates of the eastern shore of the northern flat supported mainly *Acetabularia* sp. Subtidal muddy sites of the northern flat supported *Halophila ovalis* meadows with varying degree of cover. Shallower mud substrates were variously covered by *Chaetomorpha* which locally forms dense mats. *Ruppia megacarpa* occurred in small water-retaining inter-tidal depressions and undulations. Drift of *Gracilaria* spp was present on otherwise bare mud in most peripheral and inter-tidal portions of the northern flat. The muddy floor of the central basin was mostly devoid of vegetation, but a sparse or patchy cover of *Halophila ovalis* occurred locally. The sand sheets environments in the Collie delta sites were generally devoid of vegetation.

Discussion

Most of the estuary comprises the flat, deep and elongate central basin, flanked to east and west by shallow, shore-parallel platforms that are related to the upslope features of relict and active dunes respectively. To the north, the central basin grades into a shallow water northern flat, and to the south deltas intrude into the estuary.

Substrate type reflects proximity to sediment source, extant processes, and grain size availability. Consequently, Leschenault Inlet is underlain by:

- mud in the central basin and northern flat;
- sand and muddy-sand on the eastern platform, where there is local reworking/winnowing of shore materials in this wave dominated environment;
- sandy-mud, mud, muddy-sand and sand on the western platform where dune sand encroaches into and contributes sand to the estuary, and where more mud accumulates than on the eastern platform because of its more sheltered nature; and
- sand in the deltas.

The estuary is generally of marine salinity and vertically well mixed. The hydrochemistry is dominated by daily

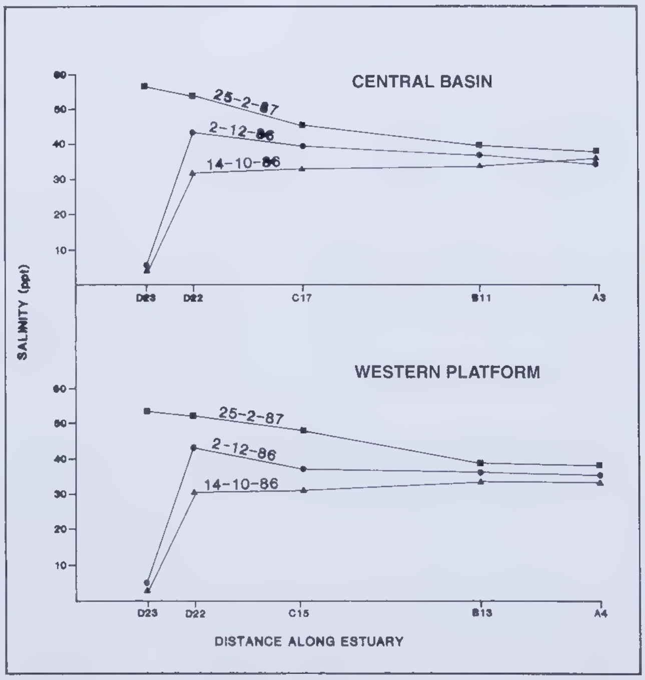

Figure 11. Graph of salinity along the length of the Leschenault Inlet, at three sampling times during this study, for sites on the a) Central Basin; b) Western Platform.

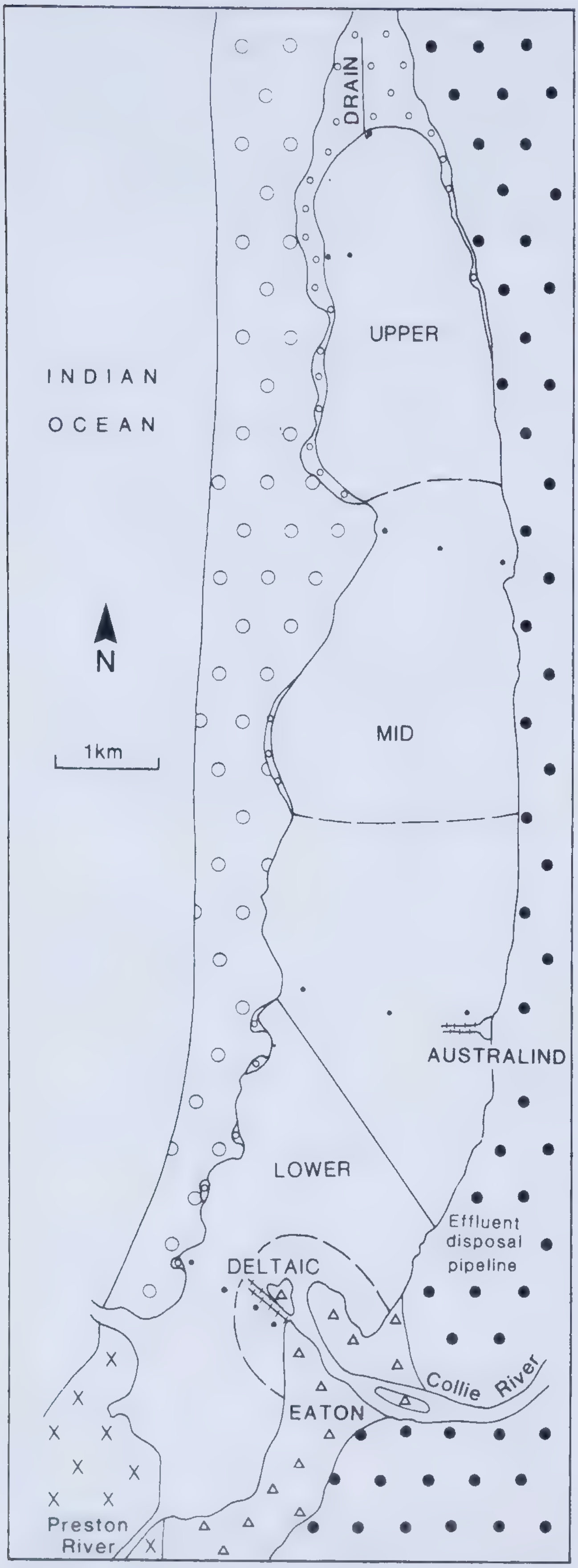

Figure 12. Proposed estuarine salinity fields of Leschenault Inlet, based upon values for the range and mean (± sd) of water salinity data at water quality monitoring sites during this study (See also Table 5). The location of monitoring sites is shown in Fig 2.

exchange through the artificial channel and wind- and tide-forced circulation. However, the estuary is still poikilosaline, due to freshwater inflow during the winter in the south, and restricted oceanic exchange and summer evaporation in the north. In this respect Leschenault Inlet is similar to estuaries elsewhere in south-western Australia.

In winter, salinity of the estuary decreases with fresh water input, from rivers, drains, run-off from adjoining terrain, and groundwater seepage from upland aquifers (*e.g.* dunes; Semeniuk & Meagher 1981b) and deltas. These studies indicate that after the cessation of fresh water input, evaporation (induced by summer temperatures and wind), and the continued limited exchange with the ocean become important determinants of water salinity to the north, away from "The Cut", which may become hypersaline. There is a salinity gradient from south to north for most seasons.

Values of the mean and standard deviation of water salinity (Table 5) can be used to describe salinity fields within the estuary. As data were collected at only 4 transects along the length of the estuary, and because it is expected that the salinity trends are gradational, the boundaries between fields can only be interpolated. However, the Leschenault Inlet water body may be divided into 4 gradational salinity fields, based on mean salinity values and the variation in the salinity developed throughout the year (Table 5). These are (Fig 12):

- the deltaic field which has a mean salinity value of slightly less than sea water but a large variation about the mean (*e.g.* Transect A sites 1,2; Table 5);
- the lower estuarine field in which a mean salinity value slightly greater than sea water is maintained, with a small variation about the mean (*e.g.* Transect A sites 3,4,5,6,7; Table 5);
- the mid estuarine field in which a mean salinity value higher than sea water is maintained, with a large variation about the mean (*e.g.* Transect B& C sites, Table 5); and
- the upper estuarine field in which a mean salinity value much greater than seawater is maintained, with a very large variation about the mean (*e.g.* Transect D sites, Table 5).

Habitat types

Nineteen (19) small-scale habitat types within Leschenault Inlet are proposed (Fig 13). These have been determined by interactions between the 5 large-scale geomorphic units (Fig 3) and large-scale estuarine salinity patterns (Fig 12). The habitats are named, and further differentiated, according to large-scale geomorphic setting, substrate, presence of macrophytes and salinity field. A description of the 22 monitoring sites in terms of the habitats is presented in Table 6.

The northern flat lies within the upper estuarine salinity field, where there are four small-scale habitats (Table 6, Sites D20, 21, 22; Fig 9 Transects M, N & O). These are: 1. inter-tidal mud; 2. inter-tidal sandy mud; 3. vegetated flat mud; and 4. vegetated flat sandy-mud.

The central basin spans the mid and lower estuarine

Table 5. Ranges and mean + sd of water temperature (°C), oxygen concentration (mg L^{-1}) and salinity (‰) in Leschenault Inlet at sites along Transects A-D. Only data from sites sampled during the 1986-87 study period were used to calculate mean and standard deviation. For maxima and minima, all available data, including Anon 1982a, Anon 1982b, and Anon 1985b, were used from locations used in this study (Refer to Table 1a for information on sampling times).

		Temperature (°C)		Oxygen (mg L^{-1})		Salinity (‰)	
		Max & Min	**Mean ±sd**	**Max & Min**	**Mean ± sd**	**Max & Min**	**Mean ± sd**
Transect A	1	17.5 - 30.0	22.4 ± 4.1	7.6 - 14.2	9.8 ± 2.1	17.5 - 41.5	31.5 ± 7.3
	2	17.0 - 27.0	21.7 ± 3.1	6.0 - 11.0	8.9 ± 1.6	15.0 - 39.5	33.1 ± 6.1
	3	14.0 - 28.5	20.4 ± 2.5	6.0 - 1.0	8.4 ± 1.6	4.7 - 42.5	36.1 ± 2.0
	4	16.5 - 24.5	20.8 ± 2.3	6.2 - 12.2	8.5 ± 2.0	20.5 - 43.5	36.3 ± 2.4
	5	16.5 - 28.5	-	8.7 - 13.3	-	33.5 - 41.5	-
	6	17.5 - 24.5	-	11.9 - 12.0	-	24.0 - 34.5	-
	7	15.5 - 23.0	-	9.7 - 13.8	-	21.5 - 34.5	-
Transect B	8	16.5 - 30.0	-	8.7 - 15.3	-	32.0 - 45.5	-
	9	16.5 - 27.0	22.4 ± 3.0	7.0 - >20	10.7 ± 3.3	23.5 - 45.0	37.8 ± 3.6
	10	16.5 - 24.5	-	6.8 - 11.6	-	32.5 - 44.5	-
	11	12.5 - 26.5	21.1 ± 2.2	5.0 - 10.8	8.3 ± 1.5	17.0 - 45.4	37.3 ± 3.3
	12	16.0 - 25.5	-	5.9 - 10.2	-	29.5 - 44.5	-
	13	17.0 - 29.5	22.6 ± 3.3	7.0 - 11.8	9.4 ± 1.5	32.0 - 46.0	36.4 ± 3.2
	14	17.0 - 33.0	-	10.5 - 14.8	-	31.5 - 45.5	-
Transect C	15	17.5 - 31.5	24.6 ± 4.1	9.4 - 19.0	11.7 ± 2.8	28.5 - 48.5	39.9 ± 6.1
	16	17.5 - 31.0	-	10.9 - 14.8	-	30.0 - 47.5	-
	17	11.0 - 27.5	21.8 ± 2.6	3.9 - 12.5	9.3 ± 1.5	17.0 - 46.0	39.0 ± 5.4
	18	17.0 - 32.0	24.6 ± 4.3	10.5 - >20	14.4 ± 3.5	30.0 - 47.0	38.0 ± 4.8
	19	16.5 - 29.5	-	10.3 - 11.9	-	25.5 - 48.0	-
Transect D	20	17.0 - 30.0	22.9 ± 4.6	6.6 - 16.2	9.6 ± 2.6	21.0 - 62.0	45.2 ± 10.2
	21	17.5 - 32.0	-	8.3 - 13.3	-	21.0 - 48.0	-
	22	17.0 - 31.0	23.0 ± 4.5	8.0 - 14.6	10.4 ± 3.0	21.0 - 62.0	44.5 ± 9.6
	23	10.5 - 27.0	-	5.0 - 11.0	-	18.4 - 53.6	-

Table 6. Habitat features of sites on Transects A-D.

Site	Habitat unit	Large-scale geomorphic unit	Substrate	Flora	Salinity field
A1	Deltaic inter-tidal sand	Collie River Delta	Medium & coarse sand	None	Deltaic
A2	Deltaic sand	Collie River Delta	Medium & coarse sand	None	Deltaic
A3	Lower estuarine basinal sandy mud	Central Basin	Sandy mud	Patchy *Halophila*	Lower
A4	Lower estuarine platform	Western Platform	Muddy medium sand	*Halophila*	Lower
A5	Lower estuarine inter-tidal muddy sand	Western Platform	Muddy medium sand	Patchy algae & *Halophila*	Lower
A6	Deltaic inter-tidal sand	Collie River Delta	Medium & fine sand	Patchy algae & *Halophila*	Lower
A7	Deltaic inter-tidal sand	Collie River Delta	Medium & fine sand	Patchy algae & *Halophila*	Lower
B8	Lower estuarine platform sand	Eastern Platform	Medium sand	Patchy *Halophila* & algae	Lower
B9	Lower estuarine platform muddy sand	Eastern Platform	Medium sand	*Halophila*	Lower
B10	Lower estuarine platform muddy sand	Eastern Platform	Medium sand	*Halophila*	Lower
B11	Lower estuarine basinal mud	Central Basin	Mud	Patchy *Halophila*	Lower
B12	Lower estuarine basinal mud	Central Basin	Mud	Patchy *Halophila*	Lower
B13	Lower estuarine platform muddy sand	Western Platform	Muddy medium sand	*Halophila* & algae	Lower
B14	Lower estuarine platform sandy mud	Western Platform	Sandy mud	Patchy algae & *Halophila*	Lower
C15	Mid estuarine muddy sand	Eastern Platform	Muddy medium sand	*Halophila* & algae	Mid
C16	Mid estuarine muddy sand	Eastern Platform	Muddy medium sand	*Halophila* & algae	Mid
C17	Mid estuarine basinal mud	Central Basin	Mud	Patchy *Halophila*	Mid
C18	Mid estuarine platform sandy mud	Western Platform	Mud	*Halophila* & algae	Mid
C19	Mid estuarine inter-tidal sand	Eastern Platform	Medium sand	None	Mid
D20	Upper estuarine inter-tidal sandy mud	Northern Flat	Sandy mud	Patchy algae	Upper
D21	Upper estuarine inter-tidal mud	Northern Flat	Mud	Patchy algae	Upper
D22	Upper estuarine inter-tidal mud	Northern Flat	Mud	Patchy algae	Upper

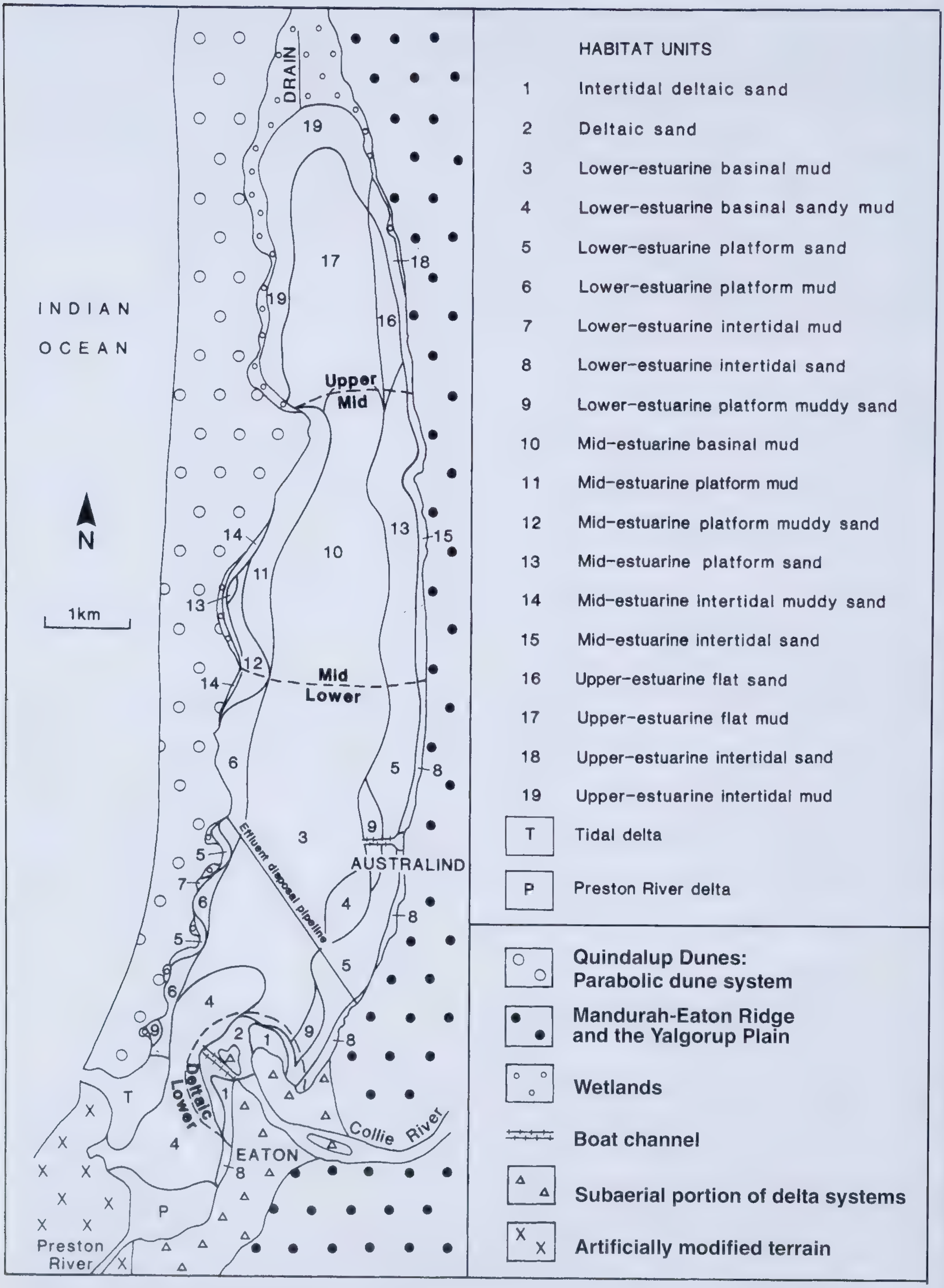
INDIAN OCEAN
N
1km
DRAIN
19
17
18
19
16
Upper
Mid
10
13
15
14
11
13
12
14
Mid
Lower
6
5
8
9
3
AUSTRALIND
Effluent disposal pipeline
5
7
6
4
8
5
5
6
4
9
2
1
9
8
T
Deltaic Lower
1
4
EATON
8
Collie River
P
Preston River
HABITAT UNITS
1 Intertidal deltaic sand
2 Deltaic sand
3 Lower-estuarine basinal mud
4 Lower-estuarine basinal sandy mud
5 Lower-estuarine platform sand
6 Lower-estuarine platform mud
7 Lower-estuarine intertidal mud
8 Lower-estuarine intertidal sand
9 Lower-estuarine platform muddy sand
10 Mid-estuarine basinal mud
11 Mid-estuarine platform mud
12 Mid-estuarine platform muddy sand
13 Mid-estuarine platform sand
14 Mid-estuarine intertidal muddy sand
15 Mid-estuarine intertidal sand
16 Upper-estuarine flat sand
17 Upper-estuarine flat mud
18 Upper-estuarine intertidal sand
19 Upper-estuarine intertidal mud
T Tidal delta
P Preston River delta
Quindalup Dunes: Parabolic dune system
Mandurah-Eaton Ridge and the Yalgorup Plain
Wetlands
Boat channel
Subaerial portion of delta systems
Artificially modified terrain

Figure 13. Map of proposed benthic habitat units in Leschenault Inlet.

salinity fields, and two small-scale habitats occur here (Table 6, sites BA3, B11, B12, C17; Fig 9 Transects E, F, G, H, I J, K, L): 1. sparsely vegetated basinal mud; and 2. sparsely vegetated basinal sandy-mud.

The western platform spans the mid and lower estuarine salinity fields, and contains the following small-scale habitats (Table 6, site A5, Fig 9 Transects E, F, G, H, I J, K, L): 1. inter-tidal sand; 2. inter-tidal mud; 3. inter-tidal muddy-sand; 4. inter-tidal sandy-mud; 5. vegetated platform muddy-sand; 6. vegetated platform mud; and 7. vegetated platform sand.

The eastern platform spans the mid and lower estuarine salinity fields and contains the following small-scale habitats (Table 6 Sites B8, B9, B10, C15, C16 C19; Fig 9 Transects E, F, G, H, I, J, K, L): 1. inter-tidal sand; 2. vegetated platform sand; and 4. vegetated platform muddy-sand.

The Collie River delta lies within the deltaic hydrochemistry field and contains (Table 6 Sites A1, A2): 1. inter-tidal sand; and 2. shallow water sand.

The intersection of geomorphology, substrate texture and detritus content, presence of macrophytes, and water salinity, has the potential to generate a variety of habitat types in Leschenault Inlet. A given environmental parameter (such as temperature, water depth, salinity) may vary gradually through space. The division between adjacent habitats may lie arbitrarily within the gradient of one or more of these parameters (*e.g.* the bathymetric junction between adjoining geomorphic units, transition between substrate types or the division between adjacent salinity fields are gradational).

This habitat classification is a first step towards linking habitat distribution and diversity with that of fauna. This framework may also be used to undertake more detailed studies of inlet attributes, and to stratify future fauna sampling programs.

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Hydrodynamics of Leschenault Inlet, Western Australia

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Abstract

A mathematical model of Leschenault Inlet and Koombana Bay was developed using finite element techniques to describe the circulation patterns in Leschenault Inlet under the influence of a variety of tidal, river inflow and wind conditions. Simulations included long term tidal characteristics, typical summer ebb and flood conditions, typical winter ebb and flood conditions and typical summer conditions with the influence of an afternoon sea breeze coinciding with a flooding tide. Tidal constituents for the Port of Bunbury, south of Leschenault Inlet provided the tidal boundary condition data for the model. The port is influenced by predominantly diurnal tides (one tide per day) with a mean spring tidal range 0.5 m. A slightly higher than mean spring tide was used for all short period simulations with a tidal amplitude of 0.3 m about mean sea level. Additionally, the four main constituents from Bunbury (M2, S2, O1, K1) were used to generate a long period of tides to assess the effect of the spring and neap tidal ranges on water levels in Leschenault Inlet. Results indicated a significant attenuation of the ocean tidal range in the inlet as well as a 4- to 7-hour phase lag for high and low water between the ocean and the inlet. These characteristics are a consequence of the hydraulic restriction presented by "The Cut". Mean water level in Leschenault Inlet was also found to be influenced by river flow and was generally higher during the winter months when flows from the Preston, Ferguson, Collie and Brunswick Rivers are higher. Circulation patterns in the inlet were found to be similar for summer and winter conditions. The afternoon sea breeze had only a minor effect on circulation patterns in Leschenault Inlet. The model has not been verified against measured current data in the inlet. Nevertheless, it provides a useful tool for comparing different tidal, wind and river flow scenarios.

Keywords: Leschenault Inlet, south-western Australia, estuary, hydrodynamics, mathematical modeling.

Introduction

Leschenault Inlet is a large coastal lagoon located just north of Bunbury, Western Australia. It is connected to the Indian Ocean by a narrow artificial passage known as "The Cut". Water levels in the inlet are influenced by tidal variations in Koombana Bay and surface drainage water from the Collie and Brunswick Rivers to the east and the Preston and Ferguson Rivers to the south. Flows in these river systems are highly seasonal.

This paper describes the circulation patterns in Leschenault Inlet under the influence of a variety of tidal, river inflow and wind conditions.

Model Development

A mathematical model of Leschenault Inlet and Koombana Bay has been developed using finite element techniques from the RMA suite of software (King 1997). The finite element network is shown in Fig 1, with detail at "The Cut" shown in Fig 2.

The model has not been verified against measured data, nevertheless it provides a useful tool for comparing different tidal, wind and river flow scenarios.

Simulations presented herein are: long term tidal characteristics, typical summer ebb and flood conditions, and typical winter ebb and flood conditions.

There are published tidal constituents (*i.e.* the harmonic components of the tides: M2 = main lunar constituent for a semidaily tide, S2 = main solar constitu-

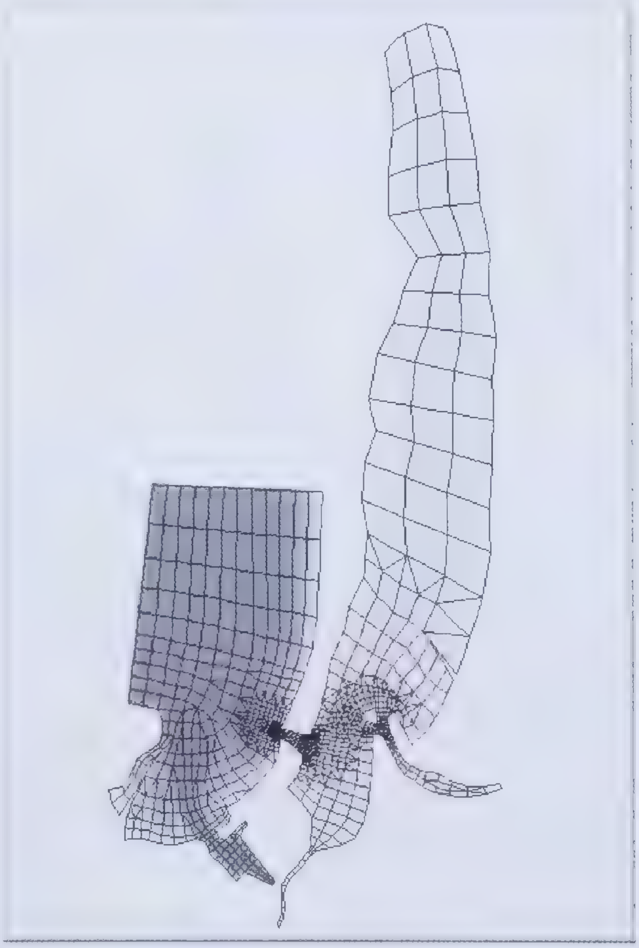


Figure 1. The finite element network used in the mathematical modelling of Leschenault Inlet and Koombana Bay.

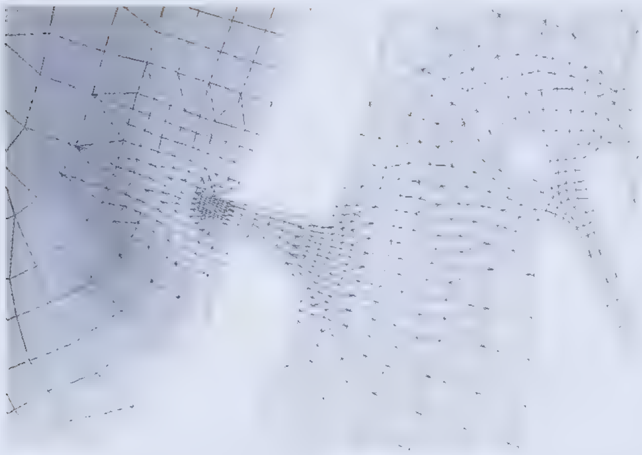


Figure 2. Computation mesh detail at "The Cut", used in the mathematical modelling of Leschenault Inlet and Koombana Bay.

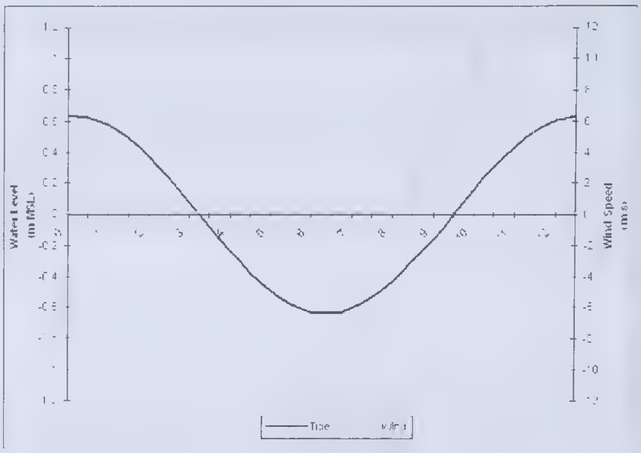


Figure 3. Tide and wind boundary conditions over a tidal cycle of 12 hours.

ent for a semidaily tide, O1 = main lunar constituent for a daily tide, K1 = soli-lunar consituent for a mainly fortnightly constituent) for the Port of Bunbury, just south of Leschenault Inlet (Anon 1997). The port is influenced by predominantly diurnal tides (one tide per day) with a mean spring tidal range 0.5 m. A slightly higher than mean spring tide has been used for all short period simulations with a tidal amplitude of 0.3 m about mean sea level. Additionally, the four main constituents from Bunbury (M2, S2, O1, K1) have been used to generate a long period of tides to assess the effect of the spring and neap tidal ranges on water levels in Leschenault Inlet.

Flows in the tributary rivers were determined by review of river flow records over the period 1985-1995. Table 1 summarises these data. The adopted flow for modelling purposes is approximately the 90 percentile value to allow investigation of typical higher flow conditions.

The influence of the afternoon sea breeze on circulation patterns in Leschenault Inlet is included. A 20 kt (10 m s^{-1}) southwest wind is simulated and is timed to coincide with the rising tide in Koombana Bay. Fig 3 shows the wind speed and tide track over a tidal cycle.

Results

A long term model simulation of 900 hours (37.5 days) was conducted to examine the effect of spring and neap tides on water levels in Leschenault Inlet. Tidal boundaries were generated from constituents as described above and "summer" flow conditions were adopted for the tributary rivers. Fig 4 presents results from the ocean, southern, mid and northern Leschenault Inlet for this long simulation. The mean water level in the inlet is higher during spring tide than during neap periods. In effect, the spring tides "pump up" the mean level in the estuary to a maximum of about 0.06 m above mean sea level while during the neap periods the mean level falls to a low of about mean sea level. Mean water level in Leschenault Inlet is around 0.03 m above mean sea level. During winter, higher river inflows tend to increase this mean level to around 0.10 m above sea level (dependent on river flow). Fig 5 shows results from the summer simulation. Water levels in the inlet and ocean are plotted along with current velocity through "The Cut".

Table 1. Summary of River Flows for the Collie, Brunswick, Preston and Ferguson Rivers (1985 to 1995)

			Flow	
		Average	90 Percentile	Adopted
Brunswick & Collie Rivers	January	7.8	10.2	60.7
	July	28.6	60.7	60.0
Preston & Ferguson Rivers	January	0.2	0.3	0.5
	July	13.9	29.9	30.0

These model results indicate a significant attenuation of the ocean tidal range in the inlet as well as a 4- to 7-hour phase lag for high and low water between the ocean and the inlet. These characteristics are a consequence of the hydraulic restriction presented by "The Cut". Peak flood tide velocities in "The Cut" occur about 1-2 hours prior to high water in the ocean and peak ebb velocities about 2-3 hours before low water in the ocean. Flood and ebb tidal flows in "The Cut" continue on for several hours after ocean high and low water respectively. Figs 6A-6D show circulation patterns in Leschenault Inlet under the influence of summer and winter river flows (respectively). Figs 6E-6F show the circulation patterns during summer with the additional influence of the afternoon sea breeze coinciding with the rising ocean tide as described above. A comparison of the model results indicates that the circulation patterns in Leschenault Inlet are very similar for summer, winter and the summer breeze condition. However, circulation patterns in Koombana Bay appear to be quite different. The eddies observed are set up by the ebb tide jet through "The Cut", the strength of which is dependent on the tidal range, wind conditions and river flow conditions. The existence of these eddies is unconfirmed, and their presence has little hydrodynamic influence on circulation patterns within Leschenault Inlet.

Numerical modelling of Leschenault Inlet and Koombana Bay indicates that Leschenault Inlet is influenced by a predominantly diurnal tide (one tide per day). A delicate balance of forces governs water movement in the Bay, "The Cut" and lower inlet (van Senden 1987) in-

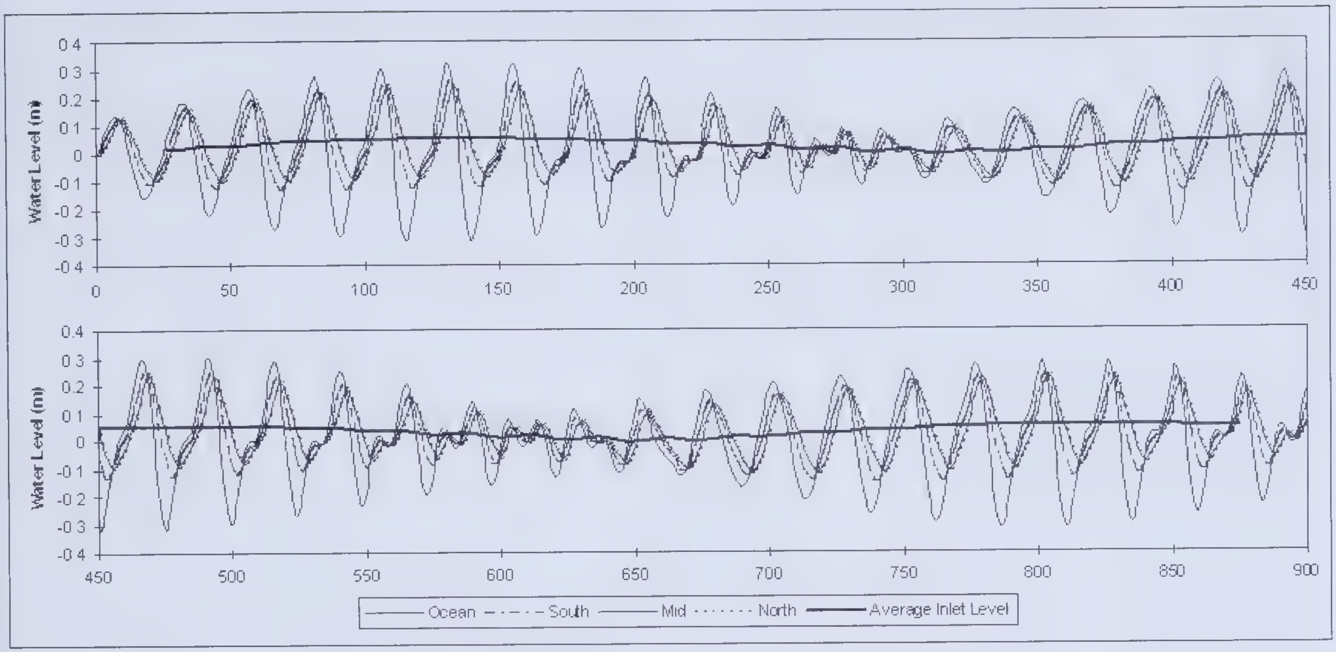
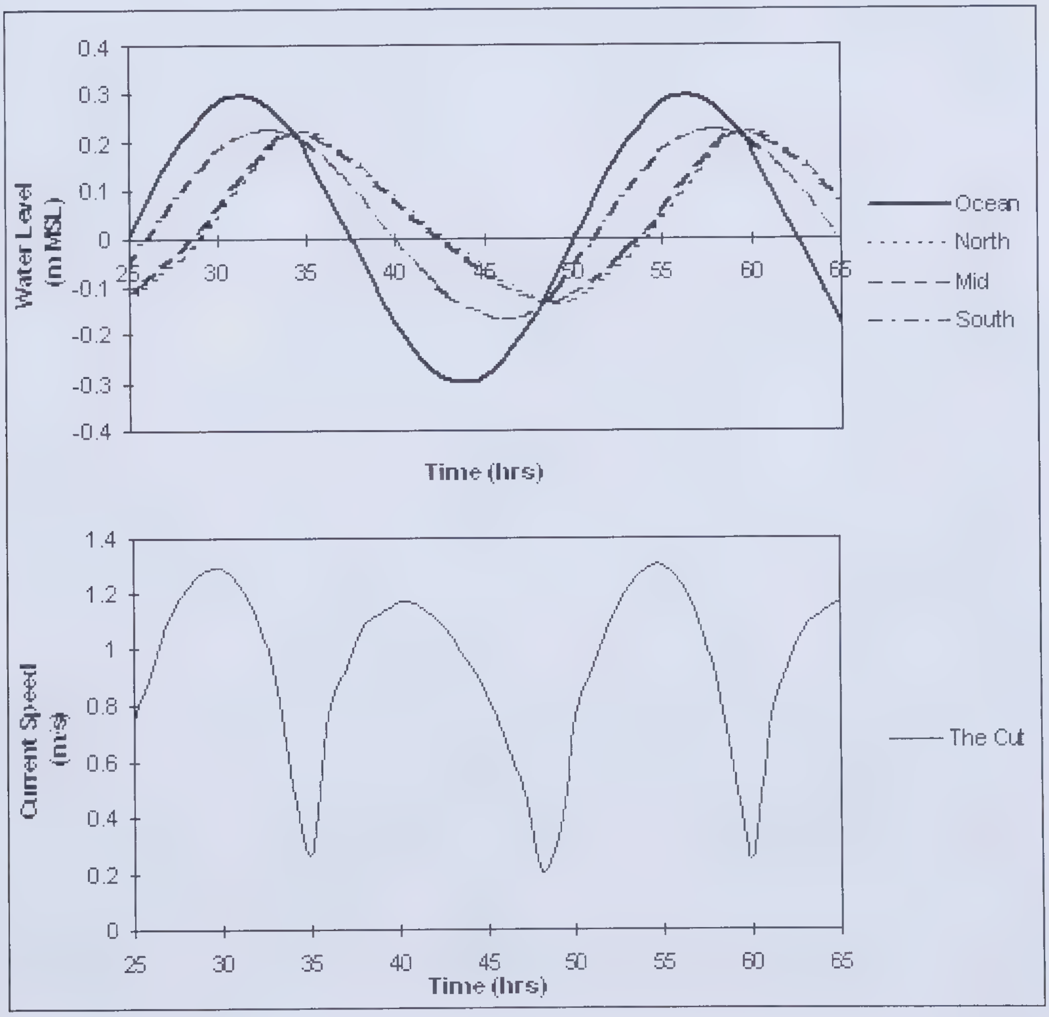


Figure 4. Mean water level variation in Leschenault Inlet over a spring tide - neap tide - spring tide cycle.

Figure 5. Flow characteristics at "The Cut" for a summer simulation. Water levels in the inlet and ocean are plotted along with current velocity through "The Cut".



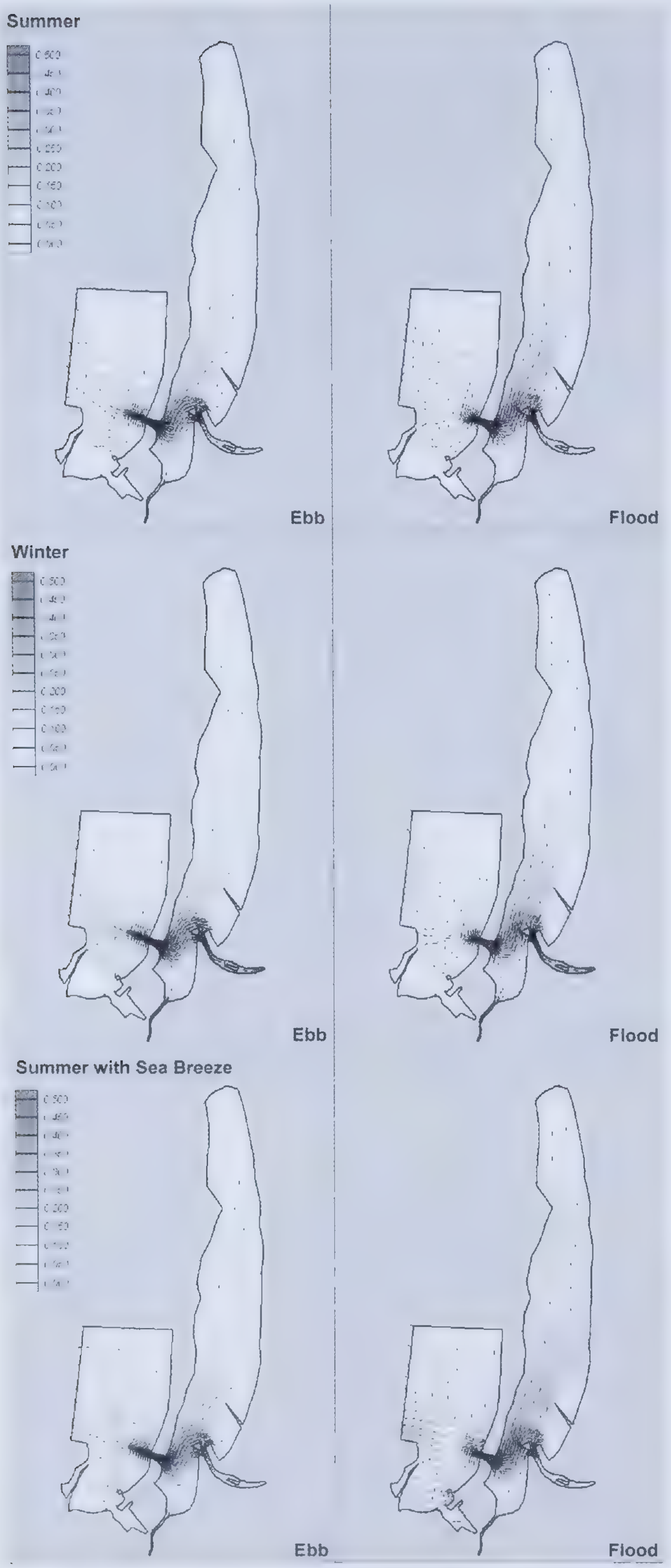


Figure 6. Circulation patterns, ebb and flood tides, for summer versus winter conditions, and summer conditions with a seabreeze. Arrows indicate direction of current. Graded shades of grey indicate magnitude of current m s^{-1}.

cluding surface wind stresses, buoyancy and momentum fluxes from "The Cut", currents induced by sea level changes, bottom friction and inertia forces due to topographic constraints. The balance of these forces has been found to vary seasonally.

Peak flood tide velocities in "The Cut" occur about 1-2 hours prior to high water in the ocean. Peak ebb tide velocities in "The Cut" occur about 2-3 hours before low water in the ocean. The mean water level in Leschenault Inlet varies and reaches a high of about 0.06m above mean sea level following a period of spring tides. Mean water level at about mean sea level occurs in the inlet following a period of neap tides. Mean water level in Leschenault Inlet is also influenced by river flow and is generally higher during the winter months when flows from the Preston, Ferguson, Collie and Brunswick Rivers are higher.

Circulation patterns in the inlet are similar for summer and winter conditions. The afternoon sea breeze appears to have only a minor effect on circulation patterns in Leschenault Inlet. The circulation patterns would result in a strong component of transport of suspended sediment that would move to the prograded supratidal flats to the far north. This northerly movement of sediment is evident as northerly directed spits and other sedimentologic factors described elsewhere in this volume.

The simple two-dimensional model described here used a coarse representation of bathymetry in the Inlet. Inclusion of a detailed bathymetry may make some difference to predictions because of the large shallow expanses along the eastern and western margins of the estuary. The magnitude of these differences is not expected to be great and is unlikely to greatly alter the circulation patterns described here.

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Sedimentology and Holocene stratigraphy of Leschenault Inlet

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Abstract

Leschenault Inlet, a shallow estuarine lagoon, is separated from the Indian Ocean by a dune barrier, with the Collie and Preston Rivers discharging to its south. Geomorphic units and their related sediments in this system include: a central basin underlain by burrowed mud; a northern basin underlain by root-structured mud; an eastern platform underlain by sand; a western platform underlain by sand; muddy sand and mud, high-tidal platforms underlain by root-structured mud; spits and bars-and-lagoons underlain by sand, muddy sand, mud, and peat; pocket beaches underlain by sand and shell grit; and the Collie River and Preston River deltas, underlain by complex arrays of sand, muddy sand, mud and peat. The lithology and sedimentary structures of the sediments are related to their formative sedimentary environment due to several factors; firstly, the nature of the shores that provide reworked material (*e.g.* quartz sand ridges of the east shore *vs* quartz and carbonate sand ridges of the west shore); secondly, local hydrodynamics (*e.g.* below wave base and thus mud-accumulating, as in the central basin; or predominately wave agitated and hence mud-free sand, as in the eastern platform); thirdly, the distribution of biota as related to the environmental conditions; and fourthly, the effects of local biota. The large scale sedimentary patterns and Holocene stratigraphic relationships in this area are relatively simple. A shore-parallel wedge of sand reworked from Pleistocene landforms is onlapped by basin mud of the central estuarine lagoon. A shore-parallel linear barrier dune complex bars and retrogrades over sediments of this estuarine lagoon. Deltaic complexes invade the southern estuary, with the Collie delta recording a deltaic sand wedge capped by muddy sediments, and the Preston River delta recording a tidal-deltaic system of shifting shoals, and intervening mud deposits. At smaller scales, in contrast to the Pleistocene-based landforms of the eastern shore, and hence simple stratigraphy, the west coast of the estuary with its dynamic barrier dunes and staggered dune encroachments has more complex stratigraphic relationships between dune sand and estuarine sediment. Also at smaller scales, the deltas consist of layered sand, muddy sand and mud in upper deltaic sequences, shoestrings of sand (cheniers) interspersed with muddy sediments, and ribbon and shoestrings of mud.

Sea level has been variable in the region over the Holocene. Relative sea level was 2-3 m lower than present between 7 000-4 500 years BP, rising rapidly to a relative position 3-4 m higher than present between 4 500 and 3 500 years BP, and progressively falling to its current level from *ca* 2 800 years BP to the present. These sea level fluctuations had an effect on sedimentation and the development of sedimentary suites and coastal landforms, particularly in their placement in relationship to current MSL.

Keywords: sedimentary, Holocene stratography, Leschenault Inlet, estuary, south-western Australia.

Introduction

As an estuarine lagoon in south-western Australia, Leschenault Inlet presents a regionally unique situation (Fig 1). It is the only estuary along this coast that has formed behind a shore-parallel barrier dune complex, and since all the other major estuaries in the southwest region have a Pleistocene ancestry, it is the only estuary that is wholly Holocene in age (*cf* the Peel-Harvey estuary, Semeniuk & Semeniuk 1990). For a small estuary, Leschenault Inlet exhibits quite a range of sedimentary environments with associated distinct sediment types. This is because there are various source types for the sediments, a range of sedimentary particles formed within the system, and a range of formative sedimentary environments and sedimentary processes operating therein.

Few estuaries along the south-western coast of Western Australia have been comprehensively described sedimentologically (*cf* the Peel-Harvey Estuary; Brown *et al.* 1980; Semeniuk & Semeniuk 1990), and as part of the collected papers on the estuarine environment of Leschenault Inlet, this paper describes the sedimentology and stratigraphy of the estuarine environment to provide an understanding of the general evolution of the estuary and the development of estuarine sedimentary suites, and to understand the processes that led to the development of the estuarine wetlands that are peripheral to the system. As such this paper provides a geohistorical framework to understanding the sedimentological development and distribution of estuarine geomorphic units throughout Leschenault Inlet that are fundamental to the development of peripheral wetland and general estuarine habitats, and relates the sedimentological evolution of the system to the Holocene sea-level history.

In this paper, the Leschenault Inlet environment is described largely in terms of its components as though there had been no anthropogenic modification of the system. Sedimentation induced by anthropogenic effects, *viz* flood tidal delta accretion, and diverted river delta accretion is briefly mentioned in context, but not described in detail.

Methods

Aerial photographs taken between 1941 and 1998 were used to document changes in the estuarine shoreline and the evolution of small scale geomorphic features. Transects through selected geomorphic units were established to describe sediment types and stratigraphy (Figs 3-7). In total some 200 sites were drilled or cored. Onshore stratigraphy was determined by drilling with a reverse-air-circulation corer to depths of 30 m, and augering and trenching to shallow depths of 1-2 m. Subaquatic stratigraphy deeper than 2 m was determined by probes and water jetting core excavation. Cores 1-2 m long were obtained from subaquatic environments to document small scale sedimentary sequences, and short cores 20-30 cm long were obtained from the main sedimentary environments to document sedimentary structures. Cores were frozen and then split to expose the sedimentary sequence and structures. Sediments were collected from the surface from a wide range of sites across the estuary as described by Wurm & Semeniuk (2000).

Sediments in the stratigraphic sequence were described under a binocular microscope in terms of colour, fabric, texture and composition. Particle size and roundness descriptions are after Wentworth (1922) and Powers (1953). Selected sediments in replicate sites of the various sedimentary suites were wet-sieved through standard Endecott sieves at 1 ϕ intervals to determine grain size distribution. Shell retained on the 2 000 mm sieve was identified as to molluscan species to determine mollusc assemblages at a given sampling site. For selected samples corresponding to samples collected from the 22 sample sites of Wurm & Semeniuk (2000), mud that passed through the < 63 mm sieve was combusted at 550 °C and 1 100 °C to determine organic carbon and calcium carbonate content, respectively. Shell samples collected for radiocarbon analyses were cleaned, acid washed, dried and then wrapped in aluminium foil for transport to commercial laboratories. Note that the term "bar-and-lagoon" refers to a sand bar and accompanying lagoon system.

Regional setting and geohistorical context

Leschenault Inlet is largely a shallow estuarine lagoon located along the coast within the southern part of the Swan Coastal Plain (Semeniuk & Meagher 1981), and located in the Leschenault-Preston Sector of Searle & Semeniuk (1985). The estuarine lagoon is separated from the Indian Ocean and Rottnest Shelf by a barrier dune system, termed the Leschenault Peninsula (Semeniuk 1985). The estuary can be classed as a microtidal barrier lagoon estuary, according to Hayes (1975). Tides are microtidal and usually diurnal, with a maximum range of 0.9 m, and a prevailing range of 0.5 m.

The study area of Leschenault Inlet is located in a subtropical subhumid climate (Koppen 1936), or Mediterranean climate (Gentilli 1972); annual rainfall is *ca* 880 mm and annual evaporation is *ca* 1 980 mm (Anon 1975).

From east to west, the three main landforms bordering and constituting the Leschenault Inlet system are (Figs 1 & 2):

1. a high ridge of Pleistocene quartz sand and limestone, referred to the Mandurah-Eaton Ridge, and to the northeast, lowlands underlain by Pleistocene limestone referred to the Yalgorup Plain (Semeniuk 1995, 1997), both of which comprise the eastern hinterland;
2. Leschenault Inlet itself, which is a elongate shore parallel, shallow estuarine lagoon; and
3. a high quartz and carbonate sand dune barrier, the Leschenault Peninsula (Semeniuk & Meagher 1981), Holocene in age, that bars Leschenault Inlet.

In addition, two deltas, the Collie River Delta and the Preston River Delta, enter the estuarine lagoon to its southeast and south (Fig 1).

The form, internal features, and the shore types of the Leschenault Inlet environment have been determined by several factors: 1. the ancestral topography of the eastern hinterland (the Mandurah-Eaton Ridge and the Yalgorup Plain) in that the former provided quartz sand to the eastern platform, and the latter forms the basis of the low tidal limestone platform to the northeast; 2. the effects of a mid-Holocene higher sea level reworking the quartz sand of the Mandurah-Eaton Ridge; 3. orientation and longitudinal extent of the Leschenault Peninsula barrier dunes; 4. the eastward migrating parabolic dunes encroaching onto the west estuarine margin from the barrier dune complex; and 5. deltaic buildups at the Collie River and Preston River mouths.

Stratigraphic framework

The stratigraphy of Leschenault Inlet area has a bearing on the types of geological materials that frame the estuary and that have been or presently are available for erosion and distribution as sediments into the environment. The main stratigraphic units in the area (after Semeniuk 1983, 1995) are discussed in Table 1.

Holocene units are shown diagramatically in Fig 2.

Source of sediment types

There are 8 main sources of sedimentary particles that contribute to the sediment types in Leschenault Inlet. These are:

1. quartz sand derived allochthonously by erosion from the ridge of Eaton Sand along the eastern shore of the estuarine lagoon; this tends to be fine to medium and moderately rounded;
2. quartz and carbonate sand derived allochthonously from the Holocene barrier dunes, by wave erosion along the western estuary shore, by transport into the estuary as mobile dunes, or transported by wind as a short range suspension deposit; this sand tends to be fine to medium and rounded; carbonate grains are skeletal debris of oceanic provenance (shell fragments, foraminifera) and limestone clasts;
3. quartz sand allochthonously injected into the estuary by the Collie and Preston Rivers flood waters; this sand tends to be fine to medium to coarse, and angular to moderately rounded;
4. phyllosilicate clay (kaolinite, smectite, halloysite, and some poorly crystalline clay), derived allochthonously

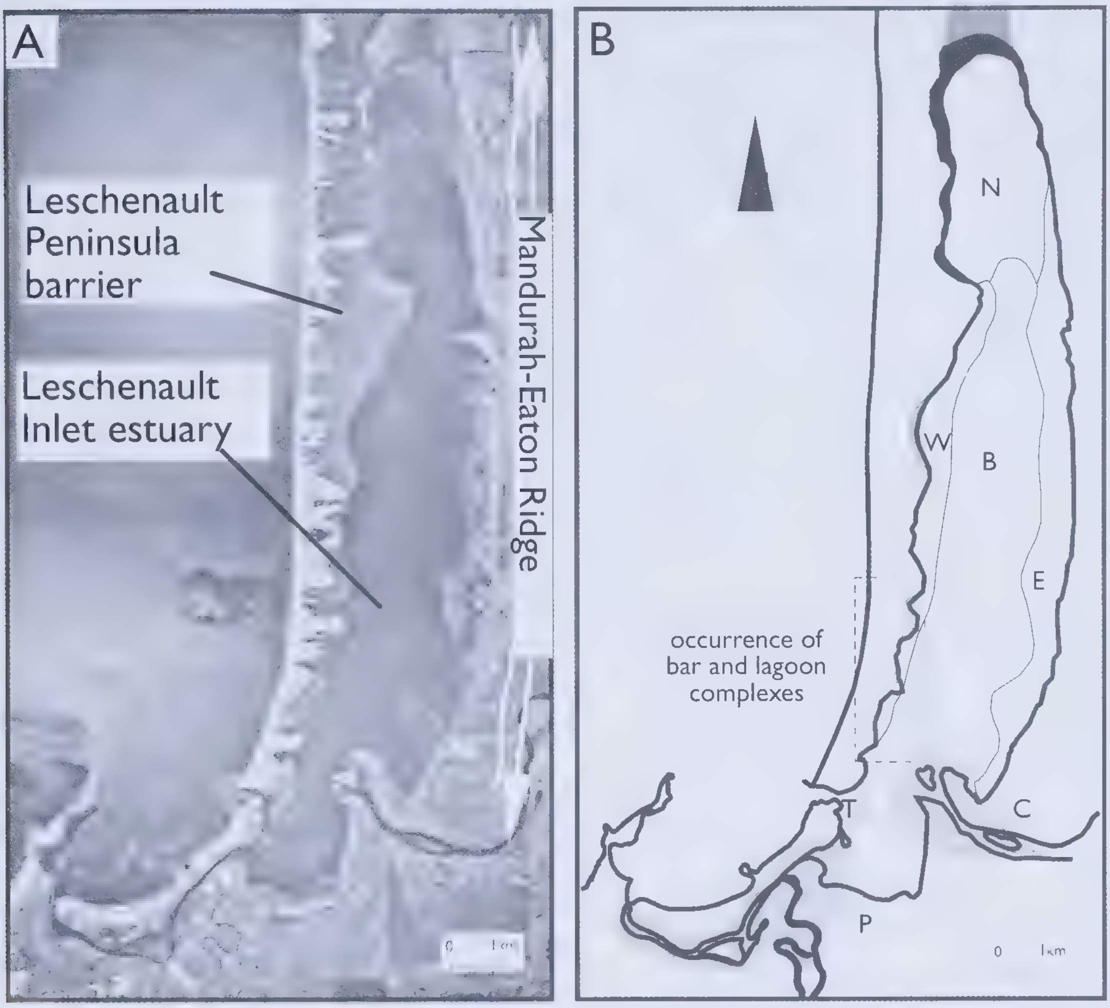
A
Leschenault Peninsula barrier
Leschenault Inlet estuary
Mandurah-Eaton Ridge
0 1 km
B
N
W
B
E
occurrence of bar and lagoon complexes
T
C
P
0 1km

Figure 1. A: Aerial photograph of Leschenault Inlet show dune barrier of the Leschenault Peninsula, the elongate estuarine lagoon, the deltas, and the eastern shore of the Mandurah-Eaton Ridge. **B:** Map showing the geomorphic components of the Leschenault Inlet estuarine lagoon. N Northern Flat; B Central Basin; W Western platform; E Eastern platform; ▨ Supratidal flat; ■ High tidal flat; C Collie River delta; P Preston River delta; ▫ Bar and lagoon complexes; T Tidal delta.

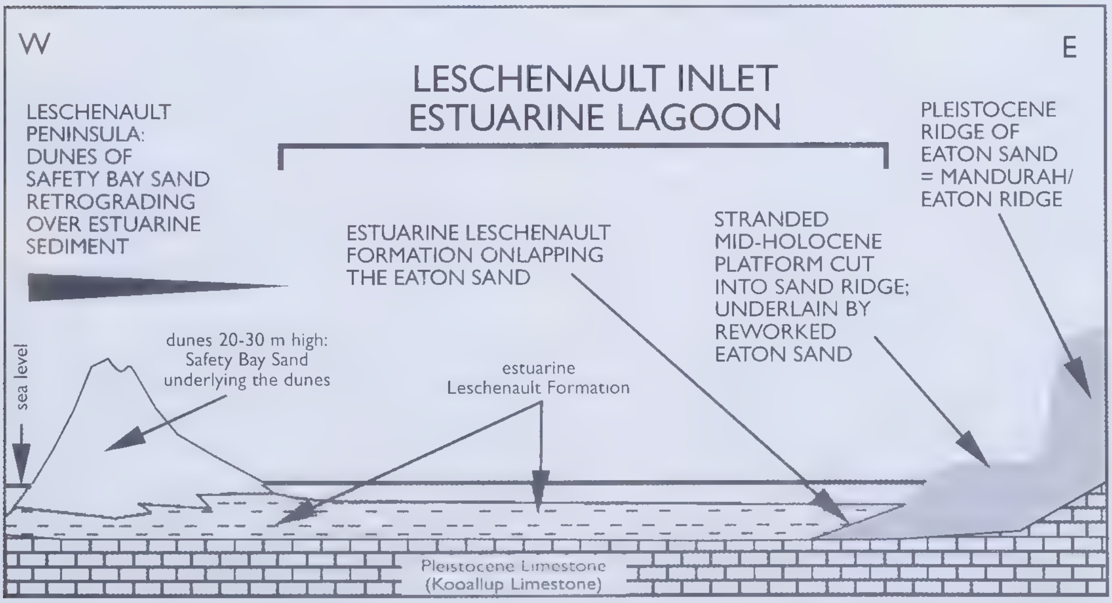
W
E
LESCHENAULT INLET ESTUARINE LAGOON
LESCHENAULT PENINSULA: DUNES OF SAFETY BAY SAND RETROGRADING OVER ESTUARINE SEDIMENT
ESTUARINE LESCHENAULT FORMATION ONLAPPING THE EATON SAND
STRANDED MID-HOLOCENE PLATFORM CUT INTO SAND RIDGE; UNDERLAIN BY REWORKED EATON SAND
PLEISTOCENE RIDGE OF EATON SAND = MANDURAH/ EATON RIDGE
sea level
dunes 20-30 m high: Safety Bay Sand underlying the dunes
estuarine Leschenault Formation
Pleistocene Limestone (Kooallup Limestone)

Figure 2. Holocene stratigraphic and geomorphic framework of the Leschenault Inlet estuary.

Table 1. Stratigraphic units in the Leschenault Inlet area in order from youngest to oldest, their ages, and their contribution as a sediment source.

Stratigraphic unit	Age	Contribution to sedimentation in Leschenault Inlet
Leschenault Formation	Holocene	part of the modern sedimentation patterns in the estuarine lagoon
Safety Bay Sand	Holocene	source for sand for the western estuarine platforms
Eaton Sand	Pleistocene	source for sand for the eastern estuarine platforms
Kooallup Limestone	Pleistocene	none
Tamala Limestone	Pleistocene	none
Australind Formation	Pleistocene	as a marl, with exposure to the south of the estuary, this partly was a source of phyllosilicate clay for the Leschenault Formation
Leederville Formation	Tertiary	none
Bunbury Basalt	Cretaceous	as a weathered body, with relief above the estuarine basin, this partly was a source of quartz and phyllosilicate clay for the Australind Formation and the Leschenault Formation

either injected into the system by flood waters of the Collie and Preston Rivers, or eroded from the southern part of the area from the Bunbury Basalt and Australind Formation;

5. carbonate silt generated autochthonously within the estuarine lagoon by accumulation of foraminifera, or by breakdown of calcareous estuarine skeletons such as molluscs, crustacea, foraminifera, and hard parts of polychaetes, and other biota;
6. silica silt generated autochthonously within the estuarine lagoon by accumulation of marine and estuarine diatoms;
7. plant detritus grading to organic ooze, generated autochthonously within the estuarine lagoon by the breakdown of plant material; and
8. shell gravel and fragments generated autochthonously in the estuarine lagoon by the shelly benthic biota, and fragmented by benthic and nektonic scavengers and predators.

Analyses of < 63 mm fraction for selected sediments in the different sedimentary environments in terms of their organic carbon content, carbonate mud, and silicate (quartz silt and clay, phyllosilicate clay, and diatoms) are shown in Table 2.

X-ray diffraction of the acid-digested carbonate-free < 63 mm fraction, and subfractions 5-63 mm and < 5 mm, shows a range of minerals to be present in the silt and clay fraction. Kaolinite, smectite, halloysite, poorly crystalline clay, muscovite and some quartz are in the clay fraction, and plagioclase, K-feldspar and quartz mainly comprise the silt fraction.

The range of sedimentary processes and synsedimentary diagenetic processes that structure and alter the sediments include; burrow structuring and bioturbation by estuarine benthos and fish; layering formed by physical reworking; grain pigmentation by iron sulphide precipitation; local carbonate precipitation forming crusts in the tidal zone; current winnowing to develop shell lag laminae; reworking of mud cliffs to form local mud clast conglomerates/breccias; and storm transport of shell from subtidal and tidal environments into the high-tidal and supratidal.

Estuarine geomorphology, sedimentary environments and processes, and sediment suites

Geomorphology and sedimentary environments

The estuarine geomorphic units within Leschenault Inlet essentially corresponds with the main sedimentary environments that form the sediment suites in the area. Geomorphology thus forms a fundamental and logical framework to describing the sedimentology in the area. The estuarine geomorphic units in the area are (Fig 1); 1. the main central basin; 2. the northern basin; 3. the eastern platform; 4. the western platform/ramp; 5. high-tidal flat platforms; 6. low-tidal flats; 7. spits, and bar-and-lagoon shores; 8. pocket beaches; 9. the northern supratidal flat; 10. the Collie River Delta; and 11. the Preston River Delta.

The low-tidal flats, spits, pocket beaches, and bar-and-lagoon shores are too small in scale to be shown in Fig 1.

In addition, there are two sedimentary units formed as a result of anthropogenic activities: 1) a small fan-shaped flood tidal delta formed leeward of an artificial channel known as "The Cut", which was excavated to facilitate exchange between the ocean and the estuary; and 2) a small fan-shaped delta formed where the Preston River diversion now enters southern Leschenault Inlet.

The central basin within the estuarine lagoon is a long, shore-parallel relatively deeper water mud-floored depression (generally 1.5-2.0 m deep). The northern basin is an oval, shallow, mud-floored depression (generally 0.5-1 m deep), that grades upslope to the northern supratidal flat. The eastern side of the estuarine lagoon where it adjoins the hinterland shore is a shore-parallel narrow, shallow water sand platform (low tidal to 1.0 m deep), vegetated by the seagrass *Halophila ovalis*, lobed on its deep water margin and straight-edged on its landward side. The western side of the estuarine lagoon where it adjoins the barrier dune is a shallow water muddy sand platform or ramp (low tidal to 1.5 m deep), also vegetated by *Halophila* *ovalis*, with a lobed deep water margin and a multiple lobed shore as a result of the encroachment of parabolic dunes into the estuary; inter-dune shores are protected small embayments underlain by mud and muddy sand.

The geomorphic nature of the eastern and western platform and ramps, *i.e.* whether the deep water margin is steeply descending (*i.e.* the edge of a platform), or gently descending (*i.e.* a ramp), can be related to the longevity and stability of the shore. The eastern platform borders a long-term stable ridge, and has developed as a wave built structure, formed and stabilised over the later Holocene. The western platform/ramp borders a dynamic shore of mobile dunes. As a result, with variable influx of sand, and varying gradients along the shore, the deep water margin of the western structure varies from steep to gentle.

In the high-tidal zone, both east and west estuary shores are mainly of saltmarsh-vegetated high tidal platforms, underlain by mud or sandy mud, and commonly terminated by a small cliff. The width of these high-tidal platforms varies from narrow (5-10 m) to wide (> 500 m) depending on location in relationship to mobile dunes *i.e.* encroaching dunes shorten their width), erosional or depositional processes (*i.e.* estuarine coastal erosion shortens their width, and estuarine high tidal mud accretion causes platform progradation), and ancestral sand ridges.

Locally, on western high-tidal platforms, often bridging interdune corridors, there are low ridges (< 20 cm high) of mud behind which there are shallow lagoons or ponds. These mud ridges appear to be accretionary, formed by wave action reworking mud deposits of the high-tidal platforms into a shore-parallel feature. On the eastern shore, above the level of high tide, there is a stranded sand platform, whose surface and margin is marked by relict sand waves, low beach ridges, and cusps. In the low-tidal zone, in front of the small cliff cut into high-tidal platforms, there is generally a gently inclined to sub-horizontal vegetation-free low-tidal flat, underlain by sand or muddy sand or sandy mud.

Along the margin of the western shore, abutting or adjoining the parabolic dune projections, there are locally developed spits, and bar-and-lagoon shores. The spits emanate from eroding dune tips, forming low relief narrow sand bodies (generally 2-5 m wide, 0.5-1 m high) projecting onto the tidal zone or the estuary, generally traversing an interdune corridor or embayment depression. Where spits have encroached fully across an interdune corridor or embayment, the tidal embayment may be barred, and a bar-and-lagoon system is formed, with the lagoon tens of metres across. Recently formed spits and bars are vegetation-free; older forms are inhabited by terrestrial vegetation of coastal dune affinities. Lagoons are open water bodies, or vegetated with rushes or samphires.

A broad supratidal flat, nearly horizontal, to very gently inclined towards the estuary, emergent by progradation, underlain by mud, and colonised by samphire, borders the northern Leschenault Inlet. The flat extends the full width of Leschenault Inlet, and has prograded some 2 km.

The Collie River has built a fluvial-dominated, to wave-modified delta where it enters Leschenault Inlet. The delta

Table 2. Analysis of the < 63 mm fraction.

Sample site	% organic Carbon	% $CaCO_3$	% silicate mud clays and siliceous diatom	Comments
southern estuary western platform	13.89	15.91	70.20	dominated by phyllosilicate clays and silica; carbonate mud and organic detritus also contribute
middle estuary eastern platform	20.83	5.68	73.49	dominated by phyllosilicate clays, silica, and organic detritus; minor carbonate mud
middle estuary central basin	12.14	5.84	82.02	dominated by phyllosilicate clays and silica; minor carbonate mud and organic detritus
middle estuary western platform	16.77	6.16	77.07	dominated by phyllosilicate clays and silica; minor carbonate mud and organic detritus
northern estuary eastern platform	14.29	19.48	66.23	dominated by phyllosilicate clays and silica; carbonate mud and organic detritus also contribute
northern estuary central basin	15.89	8.66	75.45	dominated by phyllosilicate clays, silica, and organic detritus; minor carbonate mud
northern estuary western platform	15.00	6.82	78.18	dominated by phyllosilicate clays, silica, and organic detritus; minor carbonate mud
northern supratidal flat	7.48	1.46	91.06	dominated by phyllosilicate clays and silica; minor carbonate mud and organic detritus
Preston River Delta tidal flat	12.66	32.80	54.54	dominated by phyllosilicate clays and silica; carbonate mud and organic detritus also contribute

is digitate, with storm ridges developed within the subaerial deltaic plain on its northern part where it faces the northerly to northwesterly derived winter storms. The delta is comprised of delta-front sands, a bifurcating channel, mid-channel islands, abandoned (sediment-filled) channels, levees, sub-aerial marshy flats, and stranded beach ridges and cheniers. Sand, muddy sand, mud, and peat are the main sediments that underlie the delta.

The Preston River had built a tide-dominated delta where it enters Leschenault Inlet. This delta has been partly destroyed by engineering activities, but its remnant is composed of a complex of tidal-current-aligned shoals and emergent islands, with intervening shallow channels. The islands are vegetated by samphires, rushes, and mangroves in the tidal zone, and terrestrial vegetation in the supratidal parts. Sand, muddy sand, shelly sand and shelly muddy sand (where shells are estuarine derived), mud, and peat are the main sediments that underlie this delta.

Sedimentary processes

The Leschenault Inlet environment is protected from the Indian Ocean, and hence only wind generated effects (waves, currents, aeolian action), tidal currents, and river flood currents are important.

There are three main important wind directions that generate waves on the Leschenault Inlet water body (Semeniuk & Meagher 1981): summer afternoon sea breezes emanating from the southwest (driving waves to northern sectors, obliquely impinging on the eastern shores); summer morning land breezes, of lower intensity than sea breezes, emanating from east and southeast (the latter also drive waves to the north, obliquely impinging on the north-western shores); and winter storms deriving from the northwest and north (driving waves southwards). With a fetch of 10 km in Leschenault Inlet, summer sea breezes with sustained wind speeds of up to 15 m s^{-1} (though more typically 4-6 m s^{-1}) and winter storms with wind speeds of 10-15 m s^{-1} can generate appreciable and significant wave action on the shores and shallow water sediment bodies of Leschenault Inlet. Waves trains are not of sufficient height and wave length, however, to effect significant sediment mobility in the 1.5-2 m deep central basin.

Winds also generate wind-driven currents that transport fine sediment in suspension. As a result of the dominating northerly-directed wind system (both south-westerly derived sea breezes and south-easterly derived land breezes) there is a strong net northward wind drift in the estuary. Wind further mobilises estuarine shoreline beach sand, constructing small beach ridges and dunes.

Tidal currents are locally important, despite the fact that the system is only microtidal. Their largest effect is in areas within and adjoining zones of constriction, such as the channel, shoal, and island complex of the Preston River Delta, and the artificial exchange channel ("The Cut") between the ocean and the estuarine lagoon. They also transport sand along the western shore in areas close to "The Cut".

During winter floods, the Collie River transports and injects mud-laden freshwater into the estuarine environment, and transports sand along its channel floor. The river flood current is short-lived and localised only proximal to the mouth of the delta.

The main observed physical processes that transport, shape, and develop sediment bodies in the Leschenault Inlet estuary, and their effects in shaping the sedimentary environments and developing sediment types are summarised in Table 3.

A range of biota (Fig 3) and biological processes within Leschenault Inlet contribute to and structure the sediment. The shelly benthos are often environment-specific, and hence where incorporated into the sediments are indicative of formative environmental setting. The shelly benthos that contribute gravel-sized and sand-sized material to the sediment include gastropods, bivalves, and crustacean carapaces. The extant dominant molluscs that contribute to the sediment (after Semeniuk & Wurm 2000) and the ways in which they contribute are summarised in Table 4.

There are several main environmentally diagnostic molluscan assemblages contributing shell to the sediment: 1. a mixed molluscan assemblage that inhabited/inhabits the tidally flushed environments of the Preston River Delta and the tidal delta leeward of "The Cut"; 2. a *Tellina* (-*Spisula*) assemblage inhabiting the deep water central muddy basin; 3. a *Tellina-Nassarius-Bedeva* assemblage inhabiting seagrass-vegetated platforms; 4. *Hydrococcus* populations inhabiting tidal sandy beaches; 5. *Arthritica* populations inhabiting low tidal to shallow subtidal sand flats; 6. *Tellina* populations inhabiting shallow subtidal mud flats; and 7. *Acteocina* populations inhabiting intertidal mud flats.

Earlier in the Holocene, the molluscan assemblages were markedly different in composition (Semeniuk 1983, 1985), and some of these shells have been reworked and concentrated into the modern environment. In one instance, in the central basin, current winnowing has concentrated a gravel lag consisting of the large oyster *Ostrea angasi* that accumulated *ca* 4 000 years BP (3 960 ± 200 ^{14}C years BP; GX-10548; radiocarbon laboratory: Kreuger Enterprises Inc. Massachusetts).

Apart from shell contributions, biota are also involved in sedimentary processes in Leschenault Inlet in a number of ways (Fig 3):

1. Polychaetes thoroughly rework the substrate, burrow-structuring and bioturbating the sediment; sand, muddy sand and mud sediments are bioturbated, some forming burrow-structures 1 cm diameter in the central basin muds; *Capitella*, the sand worm, is abundant on sand flats and sand platforms, *Ceratonereis*, *Capitella*, *Nephtys* and *Scoloplos* are common on the platforms, and *Capitella*, *Nephtys* and *Scoloplos* in the muds of the central basin (Dürr & Semeniuk 2000; T A Semeniuk 2000).
2. The bivalve *Tellina deltoidalis* burrows and bioturbates the aquatic platforms and central basin sediments.
3. Seagrasses in the aquatic environment bioturbate and root-structure the sediment, and contribute detritus to the sediment.
4. Rushes and samphires bioturbate and root-structure the sediments on high tidal platforms, and contribute

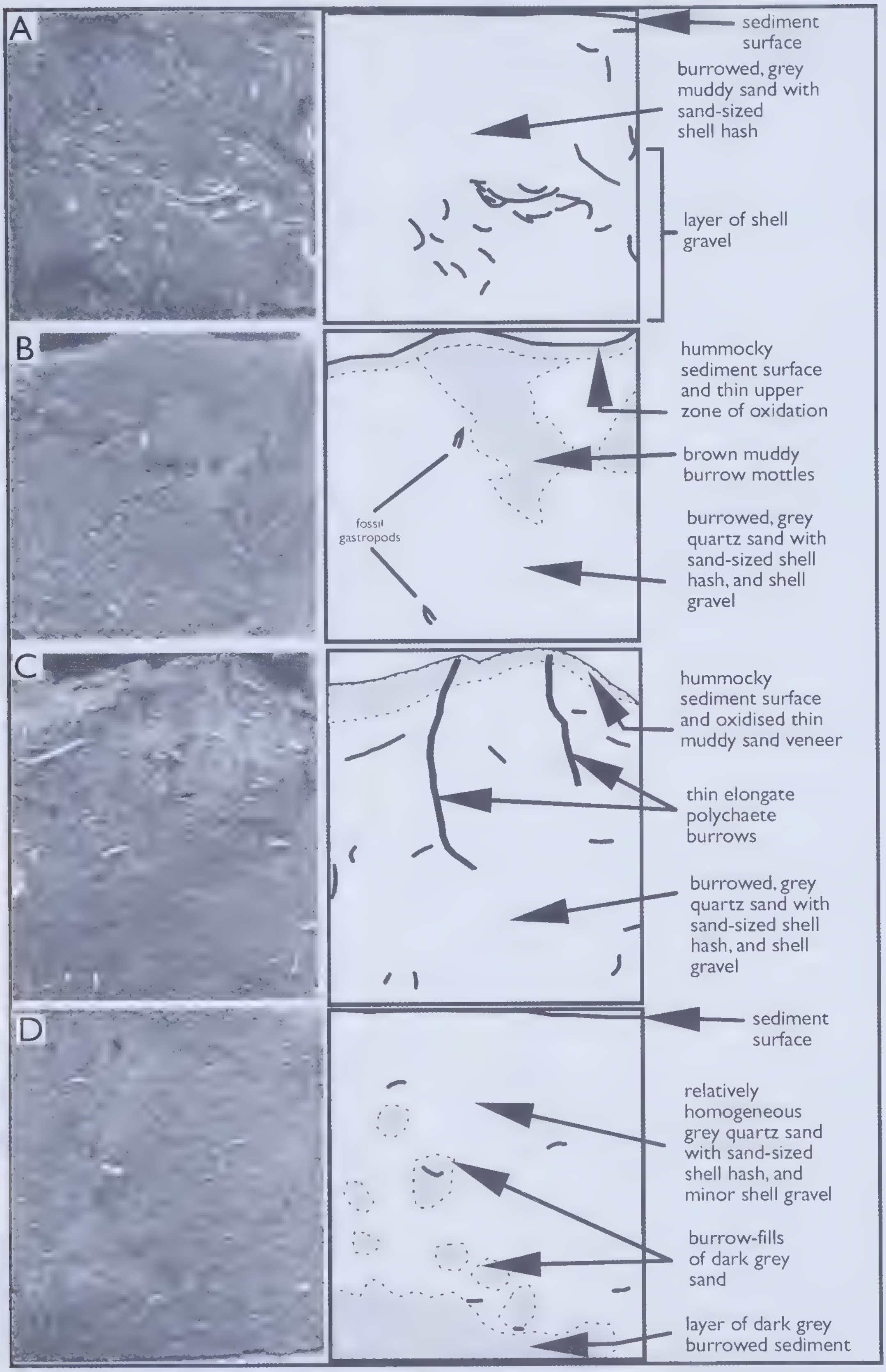
A
sediment surface
burrowed, grey muddy sand with sand-sized shell hash
layer of shell gravel
B
hummocky sediment surface and thin upper zone of oxidation
brown muddy burrow mottles
fossil gastropods
burrowed, grey quartz sand with sand-sized shell hash, and shell gravel
C
hummocky sediment surface and oxidised thin muddy sand veneer
thin elongate polychaete burrows
burrowed, grey quartz sand with sand-sized shell hash, and shell gravel
D
sediment surface
relatively homogeneous grey quartz sand with sand-sized shell hash, and minor shell gravel
burrow-fills of dark grey sand
layer of dark grey burrowed sediment

Figure 3. Photographs of sediment cores from Leschenault Inlet estuary, and accompanying line diagrams showing nature of sediments surface, sediment type, shelly components, bioturbation, and burrows. Length of cores 10 cm. **A:** burrowed grey muddy sand with sand-sized and gravel-sized molluscan shell; western platform. **B:** Burrowed quartz sand, with muddy sand mottles; shells are small gastropods reworked from earlier Holocene deposits; eastern platform. **C:** Burrowed quartz sand, with some thin elongate polychaete burrows; shell fragments are *Sanguinolaria*; eastern platform. **D:** Relatively homogeneous burrowed quartz sand, with small darker grey sandy burrow fills; minor scattered shell; eastern platform.

Table 3. Main physical processes in Leschenault Inlet estuary.

Process and main location	Main effects
wind-induced wave action on shores and east and west platforms	reworks sand on the eastern platform and generally fully removing any mud; reworks sediment on the western platform partly removing mud; erodes the sandy shores; erodes the small mud cliff shores; and shapes the surface of the eastern platform into sand waves and megaripple
wind-induced currents on east and west shores, and central basin	transports mud reworked and suspended by wave action into suspension to the northern basin and supratidal environments; transports and sorts sand, shapes the spits and bars; winnows fine sediment leaving shell lags in the basin
storm waves on east and west shores, the north-facing sector of Collie River Delta, the northern supratidal flat, and the shallower parts of the central basin	builds storm beach ridges, transports shells onto the high tide and supratidal zone, winnows sediment along the shore and in deep water central basin, and erodes the small cliff shores
tidal flooding within the Preston River Delta and the artificial tidal delta	shapes and deposits sediment on the tidal delta and Preston River Delta
tidal current erosion and transport along the east and west shores	erodes and transports sand along the shore
tidal current deposition on the high-tidal platform and the northern mud basin and supratidal flat	accumulated mud onto the high tidal environments
riverine flooding at the mouth of the Collie River	injects riverine sand and mud into the estuary
wind erosion/ transport on the east and west located sandy beaches	develops small beach ridges and dunes that fringe the estuary shore, and build the spits and bars

detritus to the sediment.

5. Amphipods and insects burrow-structure and bioturbate the sediment of both the high-tidal platforms and the aquatic platforms.
6. Fish contribute to sedimentation processes in a number of ways: predating molluscs, forming gravel shell fragments by shell breakage; contributing shell grit and mud by defaecating ingested molluscs and associated sediment; and bioturbating the substrate through scavenging and hunting.
7. The large portunid crustacean *Portunus pelagicus*, similarly, is involved in the sedimentary processes by predating and breaking molluscs, forming gravel shell fragments, and by bioturbating the substrate through scavenging and burrowing.
8. Avifauna bioturbate the shallow subtidal sediments and tidal sediments through foraging and scavenging activities.

Sedimentary environments and sediment suites

The Leschenault Inlet environment contains a range of sediment types whose characteristics directly reflect the specific geomorphological settings described earlier (Fig 4); 1. central basin and northern basin suites; 2. eastern platform suite; 3. western platform/ ramp suite; 4. high-tidal platform and northern supratidal flat suites; 5. low tidal flats; 6. spits, and bar-and-lagoon suite; 7. pocket beach suite; 8. Collie River Delta suite; and 9. Preston River Delta suite.

Spits, the bar-and-lagoon suite, and the pocket beach suite (see Fig 4C of Semeniuk & Meagher 1981) are too small to be shown in the map of Fig 4.

These sediment suites in their formative environment essentially form stratigraphic bodies (or shallow-depth sequences) with diagnostic geometry and lithologies. Though sedimentologically the suites are varied, there are dominant or characteristic sediments that typify them. The overall geometry of a suite and their characteristic sediments (without the sedimentary structural descriptors) are described in Table 5.

The full range of sediment types in the Leschenault Inlet area, further defined by their structure, fabric, texture, composition and shell content, are described in Table 6 below. Reiterating the provenance of the sand types, it is important to note that there are three types of sand in the sediments: 1. moderately rounded, fine to medium sand-sized quartz derived from the Mandurah-Eaton Ridge on the eastern shore; 2. rounded, fine to medium sand-sized quartz and carbonate derived from the Safety Bay Sand on the western shore; and 3. moderately rounded to angular, fine-, medium-, and coarse- sand-sized quartz of fluvial origin. In addition to the natural sediment suites described above, there are two locations where anthropogenic activities have resulted in an artificial riverine delta and an artificial flood tidal delta (*viz* the Preston River Diversion artificial delta suite and the artificial flood tidal delta suite).

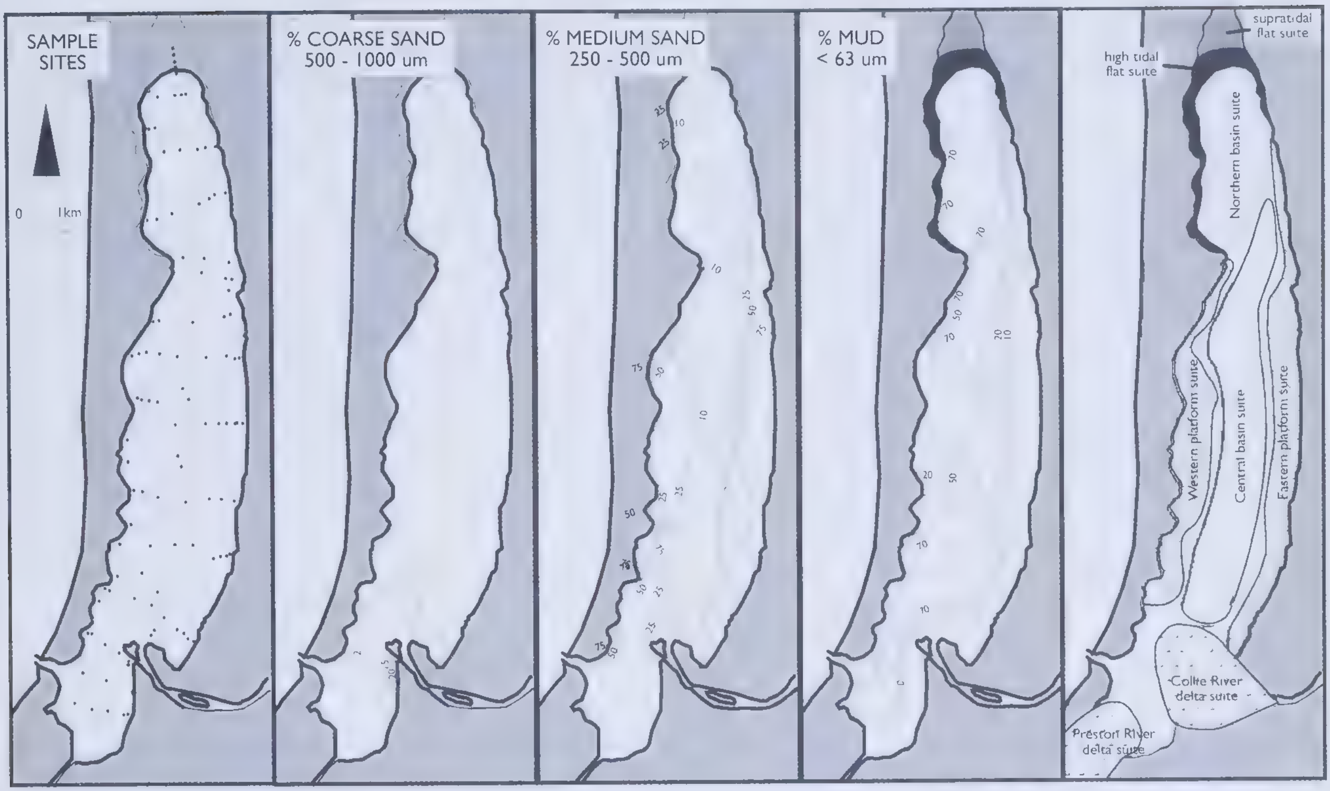

Figure 4. Maps showing sampling sites and the distribution of the coarse sand, medium sand, and mud in Leschenault Inlet (after Wurm & Semeniuk 2000). Final map shows sediment suites (or facies) based on grain sizes and geomorphic setting.

Table 4. Relationship between molluscs and sediment particles

Mollusc species	sediment particle generated
Acteocina sp	whole shell sand
Arthritica semens	whole shell sand
Bedeva paivae	whole shell gravel and fragments
Bembecium sp	whole shell gravel and fragments
Hydrococcus brazieri	whole shell sand
Nassarius (Parcanassa) burchardii	whole shell gravel and fragments
Tellina deltoidalis	whole shell gravel and fragments
Spisula (Notospisula) trigonella.	whole shell gravel and fragments
Fossil molluscs from earlier Holocene sediments	reworked whole shell gravel and fragments

Table 5. Stratigraphic attributes of the sedimentary bodies in the various suites

Sedimentary suite	shape of suite	characteristic sediments
central basin and northern basin	2 km wide ribbon	bioturbated mud and shelly mud; locally shell gravel
eastern platform	0.5 km wide wedge	quartz sand and shelly sand
western platform/ ramp	0.5 km wide wedge	muddy quartz/ carbonate sand, and shelly muddy sand
high-tidal platform	1 km wide ribbon	root-structured mud
northern supratidal flat	2 km x 2 km sheet	root-structured mud
low tidal flat sand	5-50 m wide ribbon	bioturbated mud varying to bioturbated
spits, bar-&-lagoon	small finger sands, and muddy lenses	quartz/carbonate sand, muddy sand and mud
pocket beach	thin ribbons or lenses metres wide	quartz/carbonate sand, quartz sand, mollusc grit
Collie River Delta	triangular wedge, 1 km x 1 km	quartz sand, muddy sand, mud and peat
Preston River Delta	lenses within a sheet, 2 km x 1 km	quartz sand, shelly quartz sand, muddy sand, mud

Longevity of sediment suites

Cores indicate that the various sediment suites are not just veneers in the estuarine lagoon, but are generally long term sedimentary features in the various subdomains of Leschenault Inlet (Figs 5-8). This is not unexpected, in that the controlling features developing the sediment suites in the environment are long-term stable geomorphic entities or on-going sedimentologic processes. The Pleistocene quartz sand ridge, for instance, has been a long term feature throughout the Holocene, so that it may be anticipated that that it has supplied quartz sand to the eastern platform throughout the history of the estuary. Being subject to wave trains generated by the sea breezes that would have existed throughout the Holocene, the eastern platform thus has persisted as a relatively mud-free sand platform for the duration of the estuarine conditions existing there. In the same way, the barrier dune complex that initially barred the estuarine lagoon has been a quartz/carbonate sand barrier from the onset, and has supplied this sand type to the western platform/ramp throughout the Holocene, whenever there was a western platform/ramp, or whenever a parabolic dune transgressed the width of the barrier and spilled over into the estuary. Similarly, deep water basins today, and their sediment-filled or shoaled equivalents (*viz* the northern basin and the northern supratidal flat), being deep water areas, or formerly deep water areas, and hence below base, have been long term sites for mud accumulation.

The stratigraphic cores from the northern supratidal flat, the northern basin, the eastern platform and the western margin of the western platform show that each sedimentary suite has been extant as a long term feature within the Leschenault Inlet environment, albeit with a variable sea-level history.

Sedimentological and stratigraphic evolution

The sedimentological history and stratigraphic evolution of the Leschenault Inlet system is described and discussed as follows: 1. the sedimentological/stratigraphic evolution of the system at the largest scale, *viz* the relationship of the sediments of the barrier dune to those of the estuarine lagoon; 2. the smaller scale stratigraphic interactions and relationships between the sediments of the barrier dune and estuarine lagoon; 3. small scale relationships within the deltas, and 4. the effect of a variable Holocene sea-level history on the stratigraphic evolution, and reconstruction of estuarine geomorphology over the Holocene.

Large scale relationships

The large scale sedimentary patterns and Holocene stratigraphic relationships within the Leschenault Inlet estuary are relatively simple (Figs 2 & 5): a shore-parallel wedge of sand reworked from Pleistocene landforms is onlapped by basin mud of the central estuarine lagoon, a

Table 6. Description of sediments with the various sedimentary suites.

Sediment type	Source of sedimentary particles; origin of sediment type
Central basin suite	
structureless to bioturbated mud	phyllosilicate clay, silica and carbonate mud transported by suspension; carbonate mud (silt-sized) also formed *in situ*; organic matter and detritus from aquatic plants, including silica silt from diatoms
structureless to bioturbated shelly mud	as above, but with shell from resident benthos
structureless to bioturbated sandy mud	as for the mud above, but with quartz and carbonate sand as grainfall from aeolian suspension
structureless to bioturbated shelly, sandy mud	source and origin as above, but with shell from benthic fauna
shell gravel	winnowed deposit of molluscan shell forming gravel lag pavement
Northern basin suite	
structureless to bioturbated mud	phyllosilicate clay, silica and carbonate mud transported by suspension; carbonate mud (silt-sized) formed *in situ*; organic matter and detritus contributed by aquatic plants
structureless to bioturbated shelly mud	mud as above, but with shell contributed by resident benthos
structureless to bioturbated shelly mud	mud as above; with winnowed local shell lags from resident fauna
Eastern Platform suite	
structureless to bioturbated quartz sand	sand eroded from eastern shore, bioturbated by benthic fauna
structureless to bioturbated shelly quartz sand	sand as above, with shell from local fauna concentrated in pockets and lenses
structureless to bioturbated muddy quartz sand	sand eroded from east shore, mud transported in suspension into site; detritus and organic matter from vegetation; bioturbated by benthos
structureless to bioturbated shelly and muddy quartz sand	sediment as above; shell from resident fauna; bioturbated by benthos

Table 6 Continued. Description of sediments with the various sedimentary suites.

Sediment type	Source of sedimentary particles; origin of sediment type
shell gravel	shell from local fauna; concentrated by winnowing
Western Platform/ramp suite	
structureless to bioturbated quartz and carbonate sand	sand eroded from western shore, bioturbated by benthic fauna
structureless to bioturbated shelly quartz and carbonate sand	sand as above; shell from resident fauna, bioturbated by benthos
structureless to bioturbated muddy quartz and carbonate sand	sand eroded from west shore, mud transported by suspension into site; bioturbated by benthic fauna
structureless to bioturbated shelly, muddy quartz and carbonate sand	sediment as above; detritus and organic matter from aquatic vegetation, shell from resident fauna; bioturbated by benthos
structureless to bioturbated sandy mud and muddy sand	phyllosilicate clay and carbonate mud transported by suspension; carbonate mud (silt-sized) also formed *in situ*; organic matter and detritus contributed by aquatic plants; quartz and carbonate sand contributed as grain fall from aeolian suspension
High-tidal platform and northern supratidal platform suites	
bioturbated and root-structured mud	phyllosilicate clay, and silica and carbonate mud transported by suspension; organic matter and detritus from aquatic plants; structured by fauna and vegetation
bioturbated and root-structured shelly mud	as above, but with shell deposited by storms and concentrated locally by winnowing
bioturbated and root-structured sandy mud	as above, with aeolian contribution of sand
bioturbated shelly, sandy mud	as above; shell from fauna
Low tidal flat suite	
bioturbated mud	mud transported shoreward from platform, or eroded from high-tidal mud platform; local shell contribution; reworked by biota
bioturbated sand	sand transported shoreward from platform, or eroded from adjoining upland dunes; local shell contribution; reworked by biota
Spit, and bar-and-lagoon suite	
structureless to bioturbated sand	dune sand eroded from west shore forming spits, structured by biota
laminated sand	dune sand eroded from west shore forming spits; reworked by waves and currents along beach shore
root-structured mud varying to structureless to bioturbated mud	phyllosilicate clay transported by suspension into lagoons leeward of spits and bars; structured and bioturbated by vegetation
root-structured, to bioturbated to structureless muddy sand varying to sandy mud	phyllosilicate clay transported by suspension into lagoons leeward of spits and bars; structured by vegetation; sand contributed by sheet wash from adjoining dunes, or as grain fall from aeolian suspension
Pocket beach suite (see Fig 4C of Semeniuk & Meagher 1981)	
laminated quartz sand and shelly sand	sand eroded from eastern shore, reworked in a tidal pocket beach
laminated quartz and carbonate sand and shelly sand	sand eroded from western shore, reworked in a tidal pocket beach
mollusc grit, to mollusc and quartz sand	quartz eroded from the shore; small gastropods and bivalves reworked and concentrated by wave action and storms on pocket beaches of east and west shores

Table 6 Continued. Description of sediments with the various sedimentary suites.

Sediment type	Source of sedimentary particles; origin of sediment type
Collie River Delta suite	
structureless and bioturbated quartz sand	riverine sicilic sand transported into delta; structured by biota
structureless to bioturbated shelly quartz sand	riverine sand transported into delta; shells from resident fauna or transported from adjacent environments; structured by biota
structureless to bioturbated shelly, muddy quartz sand	riverine sicilic sand and phyllosilicate clay and silica mud transported and mixed into delta; shells from resident fauna or transported from adjacent environments; structured by biota
laminated quartz sand	riverine sicilic sand transported into delta, structured by wave reworking
structureless to bioturbated muddy sand	phyllosilicate clay and riverine sicilic sand and mud transported into delta and mixed; structured by biota
structureless mud	mud as above, transported into delta
root- and burrow-structured mud	mud, as above, structured by biota
peat	accumulation of vegetation detritus
peaty sand	accumulation of vegetation detritus, mixed with sand within deltas
Preston River Delta suite	
structureless to bioturbated quartz sand	riverine sicilic sand transported into delta; structured by biota
structureless to bioturbated shelly quartz sand	riverine sicilic sand transported into delta; shells from resident mixed molluscan fauna or transported from adjacent environments; structured by biota
structureless to bioturbated shelly, muddy quartz sand	riverine sicilic sand and phyllosilicate clay and silica mud transported and mixed into delta; shells from mixed molluscan fauna or transported from nearby environments; structured by biota
laminated quartz sand	riverine sand transported into delta, structured by physical reworking
structureless to bioturbated muddy sand	phyllosilicate clay and silica mud, and riverine sicilic sand transported into delta and mixed; structured by biota
root-structured and burrow-structured mud	phyllosilicate clay and silica mud transported into delta; structured by biota
structureless mud	mud as above, transported into delta
peat	accumulation of vegetation detritus
peaty sand	accumulation of vegetation detritus, mixed with sand within delta
Preston Diversion Artificial Delta suite	
structureless to bioturbated quartz sand	riverine sicilic sand transported into delta; structured by biota
structureless to bioturbated shelly	riverine sicilic sand transported into delta;
quartz sand	shells from resident fauna; structured by biota
structureless to bioturbated muddy sand	phyllosilicate clay and silicic mud, and riverine sicilic sand transported into delta and mixed; structured by biota
structureless to bioturbated shelly,	sediment as above; shells from resident fauna;
muddy quartz sand	structured by biota
Artificial tidal delta suite	
structureless to bioturbated quartz and carbonate sand	sand eroded from the barrier dune, mobilised by oceanic waves, and transported into tidal delta on flood tides; bioturbated by benthic fauna
laminated to burrow-structured quartz and carbonate sand	sand as above, physically reworked to form lamination, and weakly burrowed by fauna

shore-parallel linear barrier dune complex bars and retrogrades over sediments of this estuarine lagoon; deltaic complexes invade the southern estuary, with the Collie delta recording a deltaic sand wedge capped by muddy sediments prograding into the estuarine lagoon, and the Preston River delta recording a tidal-deltaic system of shifting shoals, and intervening mud deposits.

The barrier and its lagoon have been extant during the middle to late Holocene for at least the past 7 000 years (Semeniuk 1985). The sheltered interior of the estuarine lagoon is accumulating mud, muddy sand, and locally sand, with estuarine shelly equivalents of these sediments. These sediments, referred to the Leschenault Formation, bear imprint of estuarine lagoonal conditions, as dark grey, or iron-sulphide pigmented, or bioturbated, or (estuarine) shelly sediments. To the east, these sediments either onlap a hinterland comprised of Pleistocene sediments, or onlap sediments derived from this Pleistocene basement, or interfinger with sediments derived from this Pleistocene basement. To the west, the barrier dune complex is comprised of a ribbon of white to cream quartz/carbonate sand, referred to the Safety Bay Sand. This barrier dune has been retreating eastwards over the estuarine sediment throughout the Holocene. The encroachment of barrier into the estuarine lagoon is through a staggered series of parabolic dune incursions that spill over into the estuary. Thus, at the largest scale, as a result of the retreat of the Holocene barrier, the Leschenault Formation sediments occupy the surface environments and underlie the extant estuarine lagoon, the Safety Bay Sand of the barrier dune overlies Leschenault Formation of the former wider estuarine lagoon, and the Leschenault Formation is exposed from under the seaward front of the retreating barrier (Semeniuk 1985).

With the net northwards transport of mud under influence of wind-driven currents, there is a general accumulation of mud in northern parts of the estuary that has resulted in the development of the expansive subtidal to supratidal mud deposits (the northern basin grading to the broad mud-underlain tidal flats, grading to the supratidal flats), and tidal deposits that developed in lee of the barrier to the northwest of the estuary (Fig 5 Transects 1 & 2, Fig 6 Transects A & B). Thus in an overview, the mud ribbon occupying the environment of Leschenault Inlet is asymmetrical, occurring in the central basin axis, but thickening to the north and northwest, and forming emergent tidal to supratidal surfaces to the north and northwest.

Smaller scale relationships

At the smaller scale, in contrast to the Pleistocene-based landforms of the eastern ridge and eastern shore, along the west coast of the estuary, because the barrier dune system is dynamic with staggered dune encroachments, the stratigraphic relationships between Safety Bay Sand dune sands and Leschenault Formation estuarine sediments are more complex (Figs 5 & 6; and Fig 5 of Semeniuk & Meagher 1981). Locally, mobile parabolic dunes rapidly and directly spill over into the estuary, forming a sandy apron in the aquatic environment, and here white Safety Bay Sand is transformed into grey Leschenault Formation sand. Lateral to this stratigraphic situation, muddy sediments of the Leschenault Formation accumulate, and later to be buried by an encroaching dune; here, white Safety Bay Sand overlies dark grey Leschenault Formation mud and/or muddy sand.

The staggered dune encroachment into the estuarine lagoon, with the laterally alternating fingers of dune sand and sheltered corridors with muddy accumulations develop a variable inter-digitating and complex interface between Safety Bay Sand and Leschenault Formation. Four types of stratigraphic sequences are generated within the Leschenault Formation at this interface with Safety Bay Sand: 1. sand aprons fronting estuary-encroaching dune tips; 2. muddy embayment fills between dune fingers; 3. the spits and bar-and-lagoon complexes; and 4. platforms and ramps extensive along the western estuary.

The Safety Bay Sand and Leschenault Formation interface is related to the position of high tide, and with the complex sea-level history in this area, this interface is variably located vertically (as will be discussed below).

Smaller scale relationships within the deltas

The gross stratigraphic array within the Collie Delta consists of deltaic sand prograding over estuarine basin mud (Fig 7), recording a deltaic wedge of sand capped by muddy sediments prograding into the estuarine lagoon. The smaller scale stratigraphic features within the delta include: 1. layered sand, muddy sand and mud in abandoned channels and inter-chenier swales in the upper deltaic sequences, correlating with the subaerial part of the delta; 2. shoestrings of sand (cheniers) interspersed with muddy sediments, correlating with the storm influenced subaerial part of the delta; and 3. ribbon and shoestrings of mud, representing abandoned channel-fills; the contact of these channel-fills with the adjoining sediments is erosional. The gross stratigraphic array within the Preston River Delta consists of lenses of shelly sand interlayered with muddy sand and mud (Fig 8), recording a tidal-deltaic system of shifting shoals, and intervening mud deposits. The fan delta in the north of the delta complex could not be sampled as it had been destroyed by earthworks in the 1960s. The smaller scale stratigraphic features within the delta include: 1. a central core of layered sand, shelly sand, muddy sand, flanked or capped by wedges or sheets of mud, correlating with a record of shoaling from shallow subtidal to high intertidal; 2. local lenses of emergent sand, recording a shoaling history from subtidal to supratidal; and 3. ribbons and shoestrings of mud, representing abandoned channel-fills.

Effect of variable Holocene sea-level history on evolution of stratigraphy

The sea level has been variable in the Leschenault Inlet area over the Holocene (Semeniuk 1985; Searle & Semeniuk 1986). Relative sea level was 2-3 m lower than present between 7 000-4 500 years BP, rising rapidly to a relative position 3-4 m higher than present between 4 500 and 3 500 years BP, and progressively falling to its current level from *ca* 2 800 years BP to the present. The relative sea level fluctuations had an effect on sedimentation and the development of sedimentary suites and coastal landforms in the Leschenault Inlet area (Fig 9). These effects are

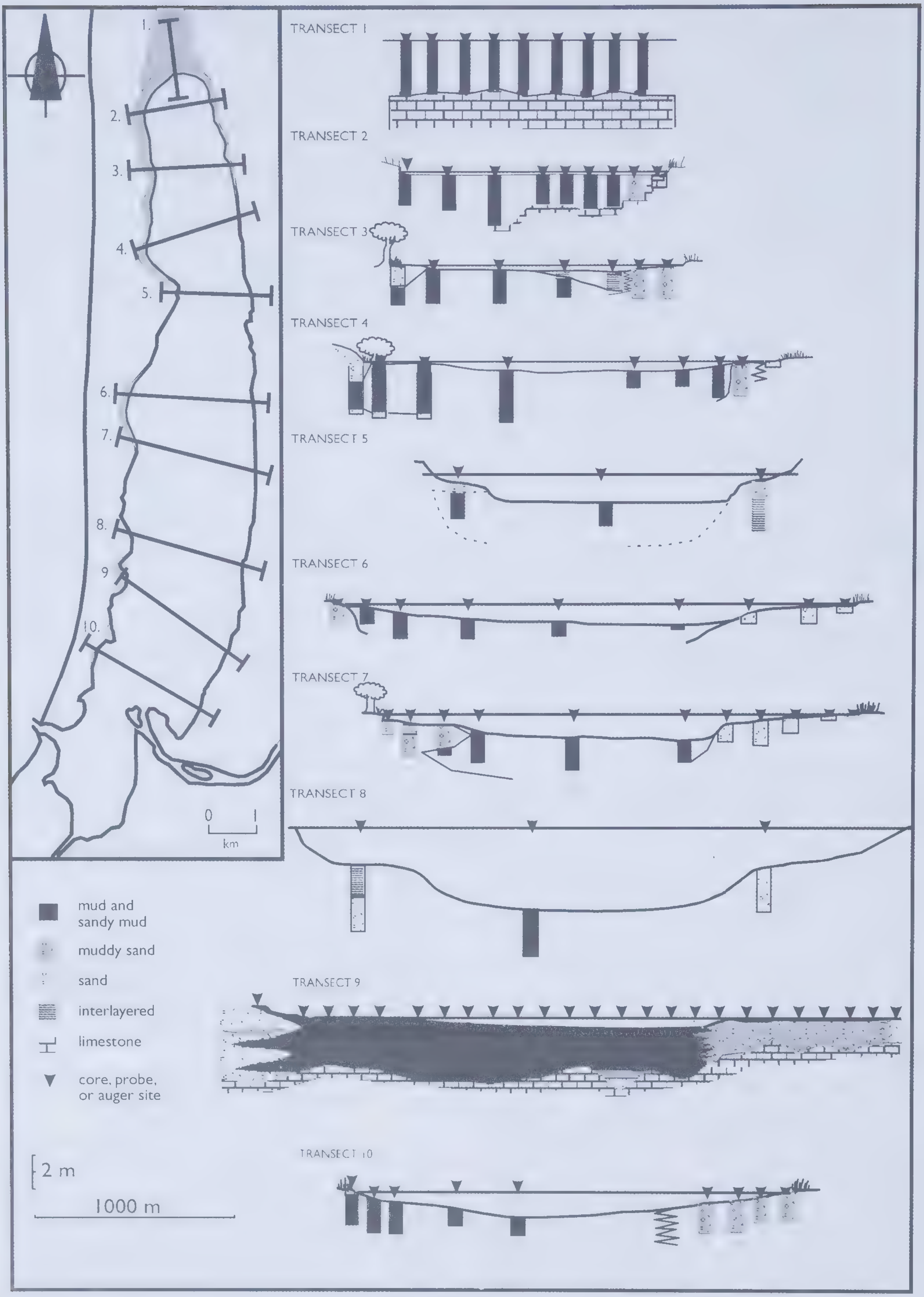

Figure 5. Various stratigraphic profiles across Leschenault Inlet, showing mud-dominated sections (central basin, north-western section, northern basin, and northern tidal to supratidal flats), and sandy to muddy sand margins.

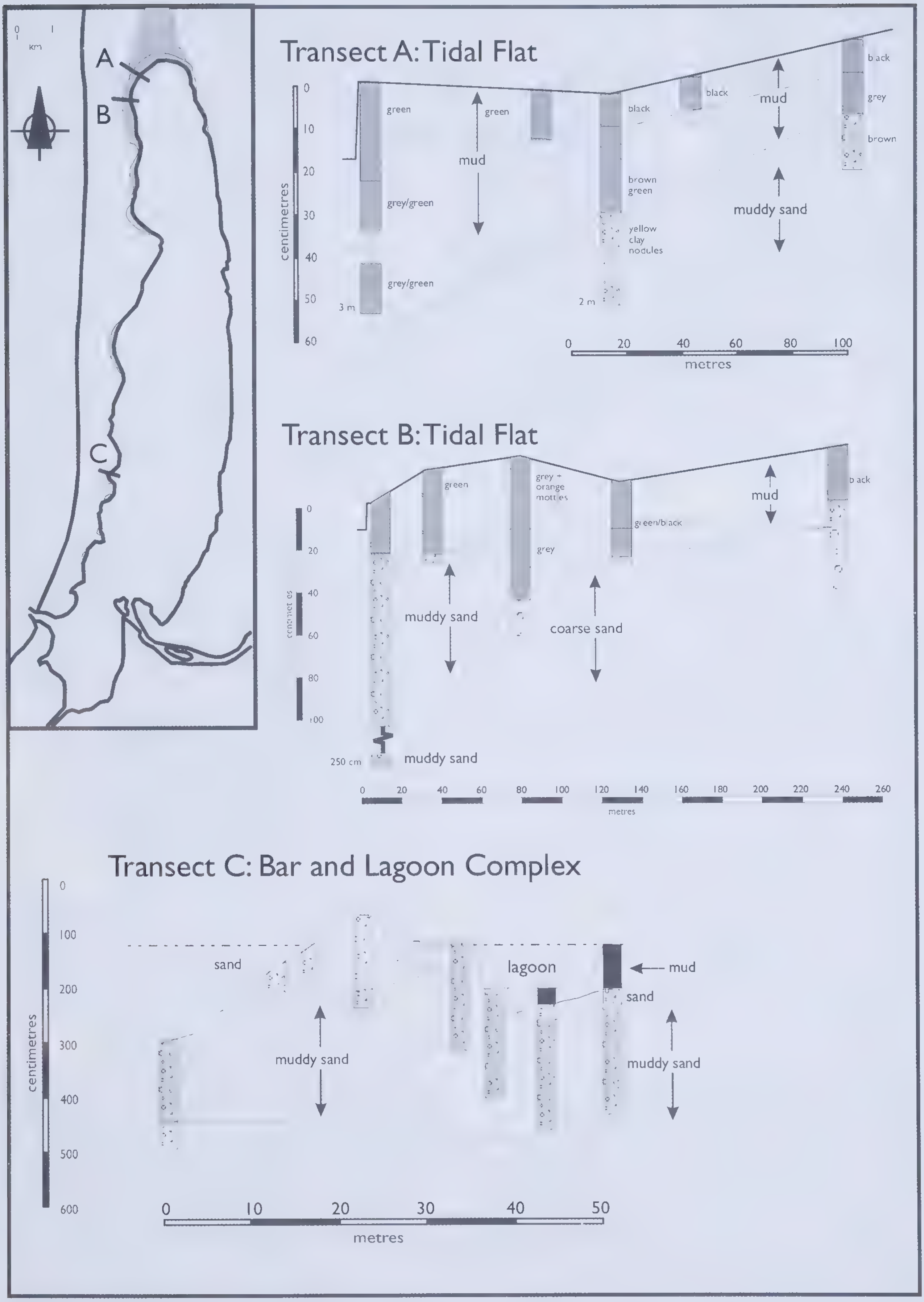

Figure 6. Various stratigraphic profiles across Leschenault Inlet showing a mud-dominated tidal flat sequences, and typical stratigraphy of a bar-and-lagoon complex.

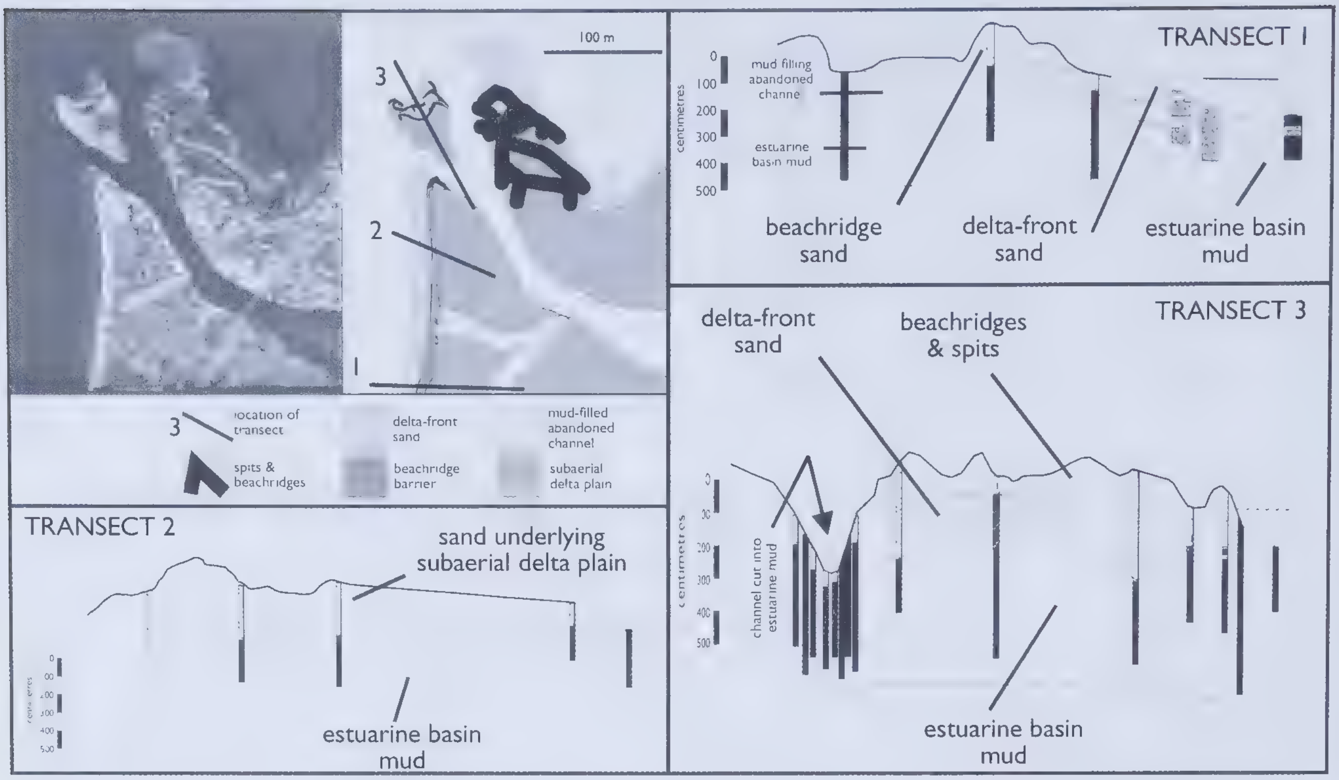

Figure 7. Aerial photographs geomorphic map, and stratigraphic profiles showing the anatomy of the Collie River delta. Interpretation of the formative sedimentary environment of the various sediment units are annotated on the cross-sections.

described for the various sedimentary environments within a framework of three stages of sea level positions *viz* Stage 1: sea level 2-3 m lower than present; Stage 2: sea level 3-4 m higher than present, and Stage 3: sea level at its present position. As will be described below, some of the details of the sedimentation and geomorphic response to a varying sea level have been documented in parts of the western platform, the eastern shore, and the central basin.

However, the details of the response of the sedimentation and coastal geomorphology to a varying sea level in this estuarine lagoonal setting must await further research. Some features of interest in this regard include, for instance, the sedimentation patterns in the deltas, the development of the spits, the bar-and-lagoon systems bordering a shallow then deeper estuarine lagoon, the response of biotic assemblages in terms of changing molluscan shell assemblages, and the mud budget within the system (*i.e.* its patterns of deposition, reworking, redispersal and redeposition).

During Stage 1, a barrier dune retreating over estuarine environments was already extant, as preserved in dune sand (Safety Bay Sand) overlying estuarine sediment (Leschenault Formation) with the stratigraphic interface located some 2-3 m below present sea level under the present barrier dune (Fig 8). Complications arising from the staggered dune encroachments into the estuary at this time are preserved as variable stratigraphic relationships between Safety Bay Sand and Leschenault Formation (*viz* thick dune sand on grey estuarine sand; thick dune sand on thick dark grey estuarine mud; thick dune sand on interlayered estuarine sand, muddy sand and mud; *cf* Semeniuk 1983).

The present central basin floor lies *ca* 2 m below sea level. Oyster shell lags on the surface dated at *ca* 4 000 years BP indicate that the mud floor probably had vertically accreted to this level *before* sea level reached the Stage 2 highstand, and that it had accreted to a level commensurate with Stage 1 sea level, and therefore that this surface was tidal or supratidal some 4 000 years BP.

For the eastern shore, for Stage 1 sea level, the surface of an eastern platform, initially developed as a wave-built structure which would have stood 2-3 m lower than its present surface. This surface would have since been buried by sand reworked to build the eastern platform structures during the higher and the present sea level stands of Stage 2 and Stage 3, respectively (see below).

Evidence for Stage 2 high-stand sea-level history is preserved in three relict estuarine sedimentary situations: as a relict western platform, as a relict eastern platform, and as relict shell beds in the central basin. For the relict western platform, estuarine shell bearing sand is preserved 1-2 m above sea level locally along the shore between the barrier dune and the estuary, indicating during the 3-4 m sea-level highstand, shelly sand beds formed on a subaqueous wave-planated dune sand terrain. Much of this stratigraphic evidence, however, has since been buried or erased by mobile sands. The evidence for the Stage 2 sea-level highstand is better developed on the eastern shore, because the ancestral sand ridge there was not dynamic and did not erase the record. Here, the eastern platform formed during the 3-4 m sea-level highstand is preserved as an elevated platform 1-2 m above present sea level (this surface would have been 1 m below sea level at the time of the highstand) underlain

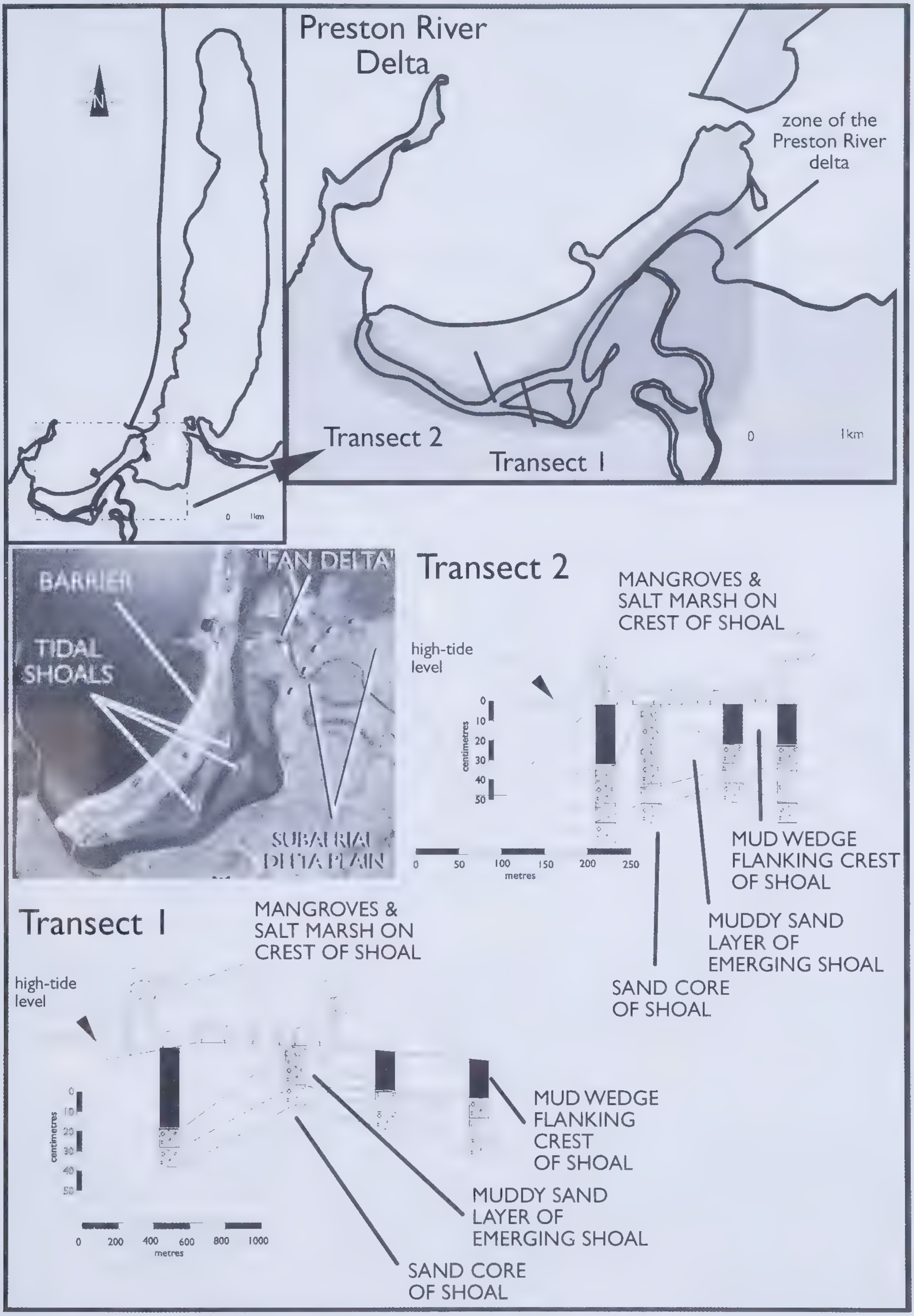

Figure 8. Aerial photograph, geomorphic map, and stratigraphic profiles showing the anatomy of the Preston River delta. Interpretation of the formative sedimentary environment of the various sediment units are annotated on the cross-sections.

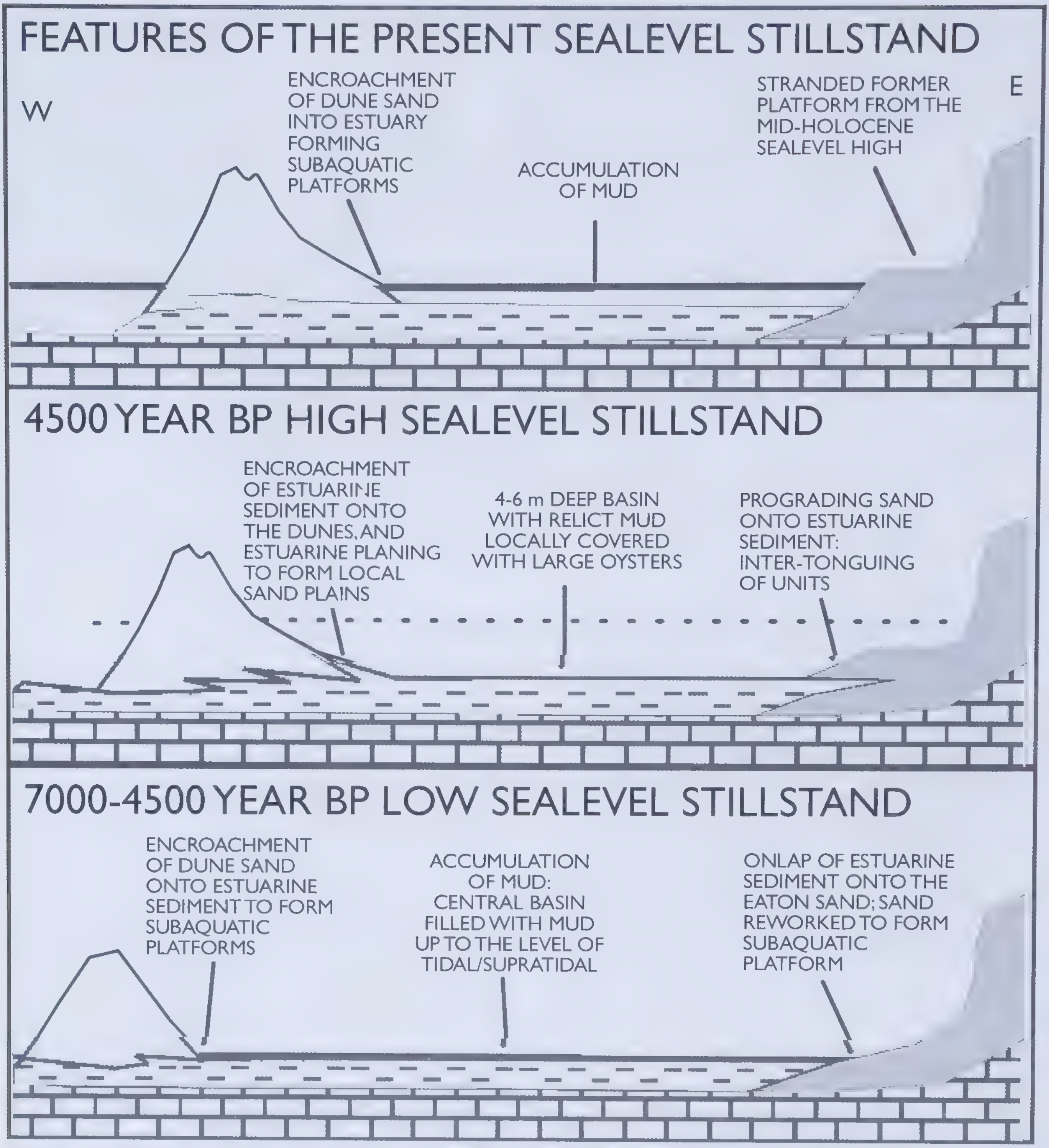
FEATURES OF THE PRESENT SEALEVEL STILLSTAND
W
E
ENCROACHMENT OF DUNE SAND INTO ESTUARY FORMING SUBAQUATIC PLATFORMS
ACCUMULATION OF MUD
STRANDED FORMER PLATFORM FROM THE MID-HOLOCENE SEALEVEL HIGH
4500 YEAR BP HIGH SEALEVEL STILLSTAND
ENCROACHMENT OF ESTUARINE SEDIMENT ONTO THE DUNES, AND ESTUARINE PLANING TO FORM LOCAL SAND PLAINS
4-6 m DEEP BASIN WITH RELICT MUD LOCALLY COVERED WITH LARGE OYSTERS
PROGRADING SAND ONTO ESTUARINE SEDIMENT: INTER-TONGUING OF UNITS
7000-4500 YEAR BP LOW SEALEVEL STILLSTAND
ENCROACHMENT OF DUNE SAND ONTO ESTUARINE SEDIMENT TO FORM SUBAQUATIC PLATFORMS
ACCUMULATION OF MUD: CENTRAL BASIN FILLED WITH MUD UP TO THE LEVEL OF TIDAL/SUPRATIDAL
ONLAP OF ESTUARINE SEDIMENT ONTO THE EATON SAND; SAND REWORKED TO FORM SUBAQUATIC PLATFORM

Figure 9. Depositional processes operating in Leschenault Inlet at the various still-stands of Holocene sealevel.

by structureless quartz sand. The sediments are free of estuarine shell (but this is not unexpected, as the equivalent sediment under the modern eastern platform are quartz rich, shell depauperate, and the stranded eastern platform since the sea-level fall to present levels has become a paperbark vegetated freshwater wetland, with peaty soils and acidic groundwater, with the attendant dissolution of any minor shells that have been present). Thus, the sedimentation event along the eastern shore during the Stage 2 sea-level highstand was reworking of the Mandurah-Eaton Ridge, and ongoing development of a higher level eastern platform underlain by quartz sand. The interlocking, of muddy sand and sand illustrated on the eastern shore at the 4 500 BP high sealevel stand (Fig 9) is preserved as thin beds of slightly muddy sand *under* the eastern platform at depth of 2m below present sea level.

With the apparently abrupt rise in relative sea level from 2-3 m below present level to 3-4 m above present level, in the central basin setting, the mud floor of a once high-tidal to supratidal surface would have been fairly rapidly inundated and placed below the zone of any wave reworking. In effect, the basin floor would have become a relict inundated high-tidal to supratidal surface and sedimentologically inactive. This mud surface, in at least 5 m of water, was the habitat for the large oyster *Ostrea angasi*. Thus, the sedimentation event in the central basin during the Stage 2 sea-level highstand was development of oyster shell beds.

With sea level at its present position (Stage 3), sedimentation involves the following main events: 1. development of the eastern platform at a new level related to the current sea level; 2. ongoing development of the western platform/ramp as parabolic dunes continue to be developed and to encroach into the estuary; 3. development of spits, evolving to bars and associated lagoons along the crenulate western shoreline; 4. development of the high-tidal platform through tidal mud accretion; 5. winnowing of mud from the subaquatic platforms and the central basin, and its transport via net northwards current drift into the northern basin; 6. shoaling of the northern basin to develop the northern supratidal flat; 7. injection of fluvial sand and mud into the estuary to develop the deltas; and 8. tidal reworking of the Preston River Delta to develop tidal-dominated estuarine landforms.

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Journal of the Royal Society of Western Australia, 83: 275-284, 2001

Sediments of Leschenault Inlet: a comparison with other estuaries in south-western Australia

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Abstract

This paper describes the properties of sediments from Leschenault Inlet, south-western Australia, and compares them with two other estuarine systems in the South West, the Swan-Canning and the Peel-Harvey. Surface sediments of Leschenault Inlet contained a large proportion of fine material, with a particle size finer than in Peel-Harvey sediments. Organic enrichment in surface sediments was higher than that in Peel Inlet, and comparable with part of the eutrophic Harvey Estuary. It was lower than central Harvey Estuary and the Swan-Canning Estuary. Sediments contained a substantial proportion of apatite P, distinctly higher than in Peel-Harvey and Swan-Canning. Concentrations of sediment total phosphorus were relatively low, but higher than in Peel Inlet. The rate of phosphorus release was low compared with the Peel-Harvey and the Swan-Canning.

Keywords: Leschenault Inlet, south-western Australia, estuary, sediments, nutrients.

Introduction

Leschenault Inlet (Fig 1) is located near Bunbury, 180 km south of Perth, Western Australia. It is a long, narrow, shallow (< 2 m) interdunal lagoon, approximately 11 km long and 2 km wide. The estuary is open to the Indian Ocean through a channel dredged in 1951.

The system is fed by two main rivers, the Collie and the Preston. The Collie, with a catchment of 3 500 km^2, is fed by the Brunswick, Wellesley and Lunenburgh Rivers from the east of the catchment. The Preston, with a catchment of 1 400 km^2, is fed by several tributaries; Ferguson River, Joshua Brook and Crooked Brook. Several dams on the two main rivers provide water for irrigation and domestic supply. Wellington Dam is on the Collie, south of Collie township, and the Glen Mervyn dam is on the upper reaches of the Preston.

The climate is Mediterranean with an annual rainfall of about 1000 mm, mainly concentrated (87%) between May and August. The average maximum temperature in winter in Bunbury is 16.8 °C (July), while in summer the average daily maximum is 27.6 °C and the average minimum is 15.1 °C. Easterly winds prevail in summer, but a strong south-west breeze occurs on most afternoons.

The Inlet has significant environmental and economic value to the region, and the waterway and its surrounds are a hub of recreational activity. It has safe, protected waters, most of which are freely navigable by small pleasure craft. Much of its popularity is due to its quality as a recreational fishing and crabbing area.

The Inlet has a diversity of ecologically-important habitats including seagrass beds, tidal mud, sand flats, salt marshes, fringing sedgelands, heathlands and *Melaleuca* woodland, with their associated biodiversity. It contains small remnant stands of the grey mangrove, *Avicennia marina*. The areas of aquatic vegetation and mangroves are nursery areas for fish and invertebrates, many of which are important to the recreational fishing industry.

The coastal plain catchment of Leschenault Inlet consists largely of sandy soils with low nutrient retention capacities (Anon 1983). Nevertheless the Inlet has been seen as a healthy, biologically-productive waterway with relatively little algal growth. There were no significant water quality problems revealed in the Collie River during monitoring in 1993-95. It has been considered one of few estuaries with a low risk of nutrient enrichment, according to the US EPA risk assessment model for estuarine eutrophication. However, the estuarine reaches of the Collie River have shown physio-chemical and biological signs of nutrient enrichment in recent years. Phytoplankton blooms of *Cryptomonas* sp and *Heterosigma akashiwo* occurred in the Collie River near its confluence with the Brunswick River in April and May 1994 (Anon 1995). There were high levels of plant biomass, comparable (on a unit area basis) with those of Peel-Harvey. Seagrass and brown algae are dominant, and appear not to be limited by nutrient availability (Lukatelich 1989; Hillman *et al.* 2000).

There are limited data on nutrient enrichment and water quality in the Inlet. Data from well-documented estuaries in south-western Australia suggest that excessive nutrient loads, and especially phosphorus and nitrogen from agricultural and urban catchments, can be a major threat to estuarine water quality and ecological health. Compared with the rural catchment, nutrient loads from the Bunbury urban area and from groundwater are relatively small. Nutrient loads entering the estuary vary from year to year corresponding to rainfall and stream flow, but it has been estimated that an annual average of about 51 tonnes of phosphorus and 610 tonnes of nitrogen enter the estuary though surface run-off from the rural catchment (Anon 1995).

Sediment is important in nutrient cycling in estuarine systems because it stores large amounts of nutrients, and may release them when the concentration in the overlying water is low (Thornton *et al.* 1995). In many cases sediment can be significant, either as a source or sink, adjusting nutrient concentrations in the water column, and so controlling primary production and the possibility of algal blooms. It is therefore important to understand the sediment properties of the estuary, and especially physico-chemical properties of the surface sediment. These matters

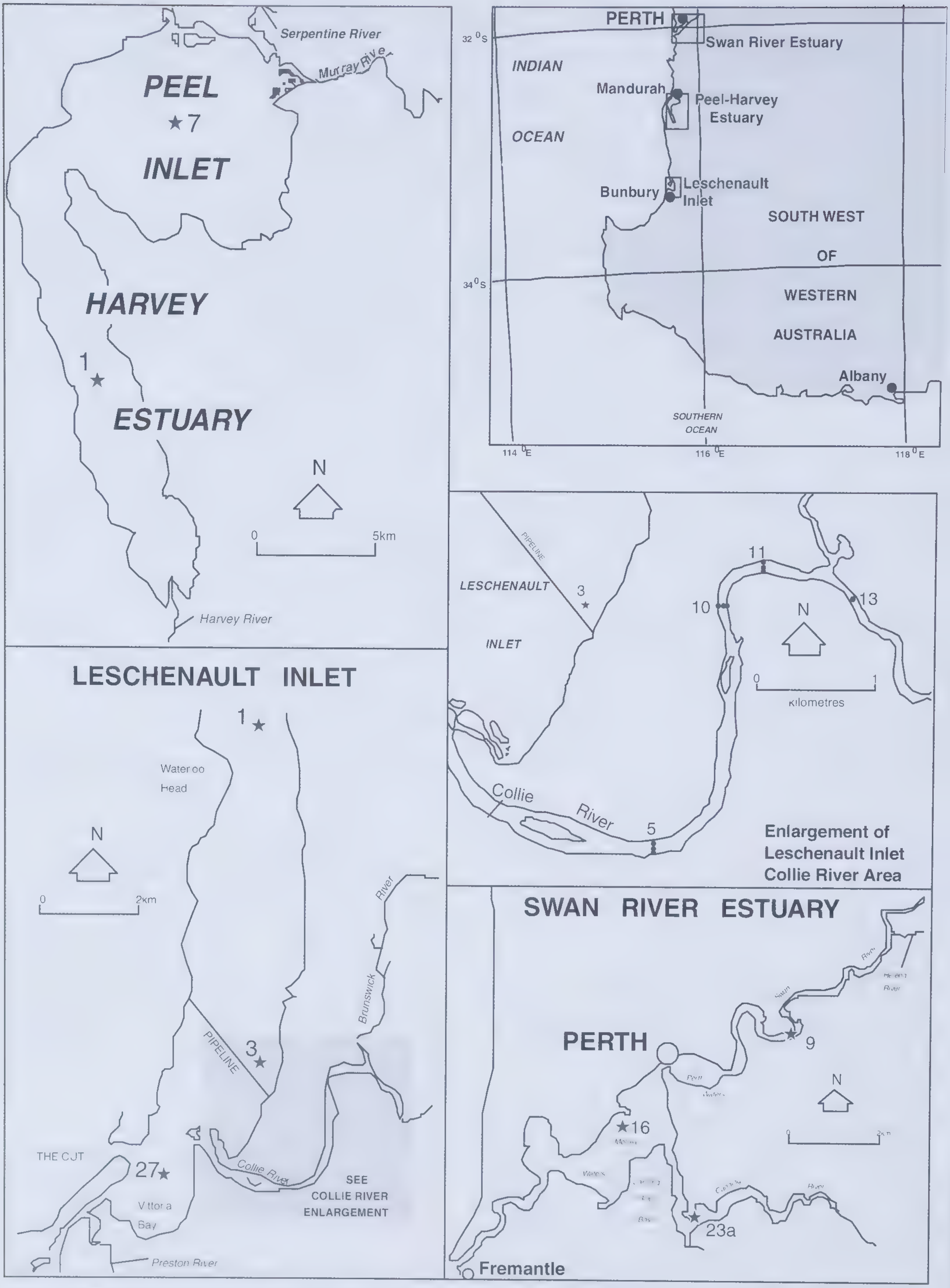

Figure 1. Sampling sites in Leschenault Inlet, Peel-Harvey, and Swan-Canning Estuarine Systems.

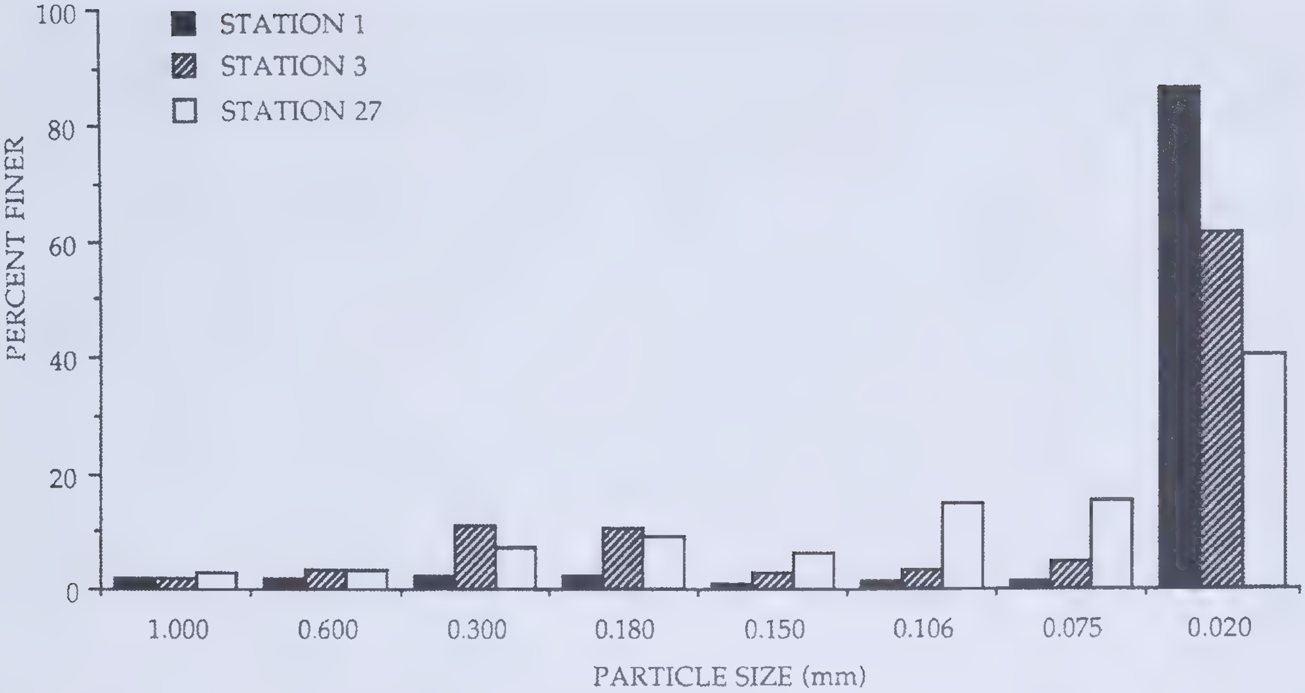

Figure 2. Particle size distribution for sediments from Leschenalut Inlet.

are addressed in this paper, which compares the sediments of Leschenault Inlet with those of others, more intensively studied estuarine systems in south-west Australia, the Swan-Canning and Peel-Harvey.

Materials and Methods

Sampling

Sediment monitoring commenced in September 1988 and continued until July 1990. Samples were taken for physical and chemical analysis from 11 sites in Collie River in July 1990, and monthly at 3 sites in Leschenault Inlet, 5 in Peel Inlet, 7 in Harvey Estuary and 6 in Swan-Canning Estuary (Fig 1).

Samples were collected from the top few centimeters by SCUBA diving, returned to the laboratory and stored overnight at 4 °C. They were dried (105 °C), ground and stored until analysis. To obtain mixed samples of surface sediment from a larger area at each site, ten sediment cores were taken from each site by pressing a perspex coring tube gently into the sediment. The upper 5 mm of sediment was extruded from the cores, placed in a bucket and well mixed. Sub-samples were stored on ice in the field and at 4 °C in the laboratory. During toxic *Nodularia* blooms in the Peel-Harvey Estuary between November and February it was not safe to dive. On three such occasions cores were therefore collected remotely using a perspex cylinder attached to a long pole operated from the boat. On these occasions only one core was taken at each site.

Intact cores were collected by SCUBA diving for metabolic work in the laboratory. A perspex cylinder, 50 cm by 9.5 cm (internal diameter), was gently pressed approximately 15 cm into the sediment. The intact sediment and cylinder were removed with the associated water column, taking care not to disturb the sediment/water interface, sealed with rubber bungs, transported to the laboratory, covered with black polythene, and incubated at 20 °C. Similar intact cores were collected from site 7 in Peel Inlet, site 1 in Harvey Estuary, sites 1, 3 and 27 in Leschenault Inlet and sites 9, 16 and 23A in the Swan-Canning Estuary.

Data recording and analysis

Wet to dry ratio (W/D) was determined by drying a known weight of wet sediment [water content = 1-(D/W)]. Percentage organic matter was determined by loss on ignition (550 °C, 1 hr).

Additional sediment samples were collected for particle size analysis. These were dried overnight (105-110 °C), weighed, and immersed in an aqueous solution of the dispersant sodium hexametaphosphate (2 g L^{-1}). The samples were periodically agitated until all sediment was dispersed. The suspension was passed through a nest of sieves which divided the particles into size classes: < 75 μm, 75-150 μm, 150-355 μm, 355-710 μm and > 710 μm. These fractions were dried, weighed and the cumulative frequency of particle size classes calculated according to Buller & McManus (1979).

Total phosphorus was determined by digesting 1 g of dried sediment with concentrated perchloric acid. Nitric acid was added first to digest volatile organic substances which may form explosive substances in the presence of perchloric acid. The released phosphate, as soluble reactive phosphorus (SRP), was measured colorimetrically with the acid molybdate/ascorbic acid reagent described by Strickland & Parsons (1972) and measured with a Varian 634 or DMS 90 spectrophotometer.

The method for phosphorus fractionation was similar to that of Williams *et al.* (1976), but without citrate-dithionite-bicarbonate (CDB) extraction. Sediment $CaCO_3$,

Table 1. Particle size distribution of sediments from Leschenault Inlet and Collie River*. See Fig 1 for site locations.

Location	Site	Q1	Median	Q3	QD	Skewness
Leschenault Inlet	1	5.8	6.0	6.2	0.2	0.00
	3	2.6	5.9	6.2	1.8	0.01
	27	2.9	4.4	6.0	1.55	-0.29
Collie River	5 (North)	3.8	4.1	6.6	1.4	-0.01
	5 (South)	0.7	1.8	5.2	2.2	0.03
	5 (Centre)	0.3	0.5	4.5	2.1	-0.28
	10 (West)	2.2	4.6	6.3	2.0	0.07
	10 (East)	1.3	4.0	6.1	2.4	0.15
	10 (Centre)	3.6	5.0	6.5	1.4	0.03
	11 (North)	0.6	1.3	2.5	0.9	0.02
	11 (South)	0.7	3.0	5.8	2.5	0.19
	11 (Centre)	1.1	2.4	5.5	2.2	0.05

Footnote: Q1 = 1st quartile (first 25% cumulative frequency as weight percentage), Median (first 50% of cumulative frequency as weight percentage), Q3 = 3rd quartile (75% of cumulative frequency as weight percentage), QD (quartile deviation); and skewness of distribution frequency.

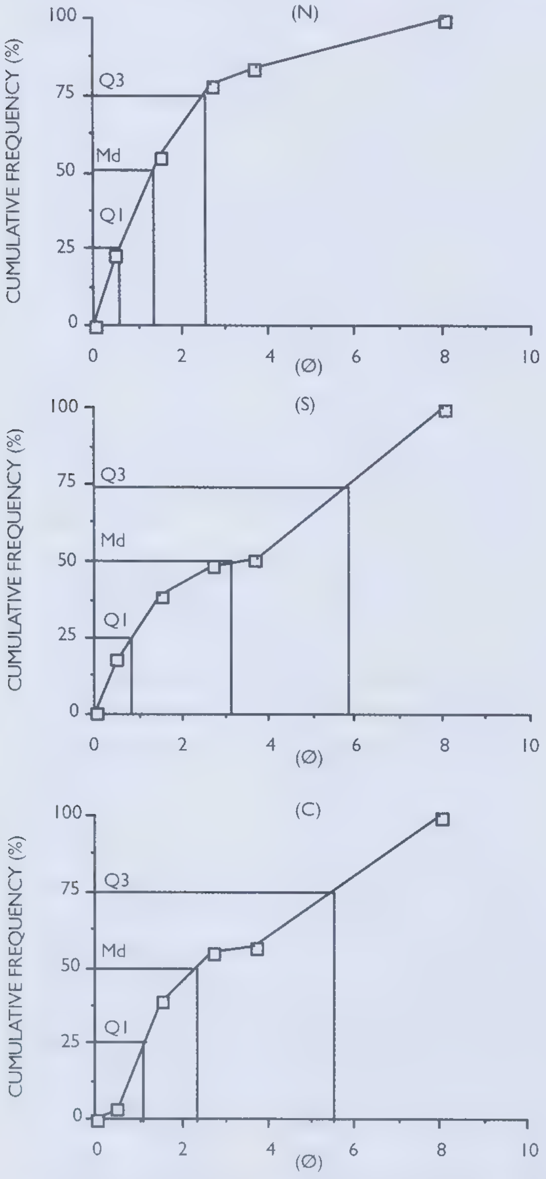

Figure 3. Cumulative weight frequency and particle diameter (Ø) for sediments from Collie River Site 11, north (N); south (S); and centre (C). Ø = - $\log_2$ (particle size mm).

Ca, Fe and Al content were analysed by the Chemistry Centre of Western Australia. Ammonia was measured by the isocyanurate method (Dal Pont *et al.* 1974).

Phosphate release rates were determined by measuring concentrations of total and soluble reactive phosphorus in the water column above the sediment in intact cores collected monthly from each estuary. Samples were withdrawn from each core on five occasions over approximately 10 days. On each occasion measurements were made of pH (Beckman Model 021), temperature, dissolved oxygen (Xertex Delta Model 4010 or Yeokal) and redox potential (Orion Model 20 meter with platinum and reference electrodes).

Results and Discussion

Sediment particle size

Particle size fractions finer than 75 µm ranged from 40.4 to 87.0% at the three sites in Leschenault Inlet. Most particles were less than 20 µm, particularly at site 1 (Fig 2).

Sediments from sites 3 and 27 had a relatively higher percentage of coarse particles and a wider range of values, reflected in the variation of the median particle size, and the quartile deviation, suggesting these sediments were poorly sorted (Table 1). The skewness values for sediments from sites 1 and 3 were near zero but a value of -0.29 for site 27 sediments suggested that the cumulative frequency of sizes was skewed towards coarse particles. There was a wide variation in median particle size (MD) for sediments from Collie River (Table 1). The average MD (in Ø) from site 10 was significantly higher than other sites, reflecting a higher proportion of finer particles with distance from the point of discharge into the estuary.

The quartile deviation in particle size distribution ranged from 0.9 at site 11 (north) to 2.5 at site 11 (south), indicating a significant difference in the level of particle-sorting force in transects across the Collie River (Table 1). This can be attributed to changing velocity of the flow around river bends, across banks and in depressions on the river bed. Seasonal flooding of the Brunswick River, carrying a large volume of silty water, enters the Collie River about 500 m upstream of site 11. The merging of the two streams increases scouring of the riverbed downstream, and forms 'high energy' sites which favour only sedimentation of larger and coarser sediments; and some 'low energy' sites which favour sedimentation of finer particles. There would thus be significant differences in flow velocity and "energy" levels across the river, and the sediments would be poorly-sorted in some regions and well-sorted in others.

The particle size distributions of Collie River Site 11 are illustrated in Fig 3. The third quartile values were relatively high at all sites, with the exception of site 11 (north). This suggests that finer particles accumulated in most sampling areas of the river bed of the Collie River.

The skewness of particle size distribution indicates, in comparison to a sample considered completely mixed, the presence of size classes over- or under-represented. The skewness values varied significantly at all sites, a positive value indicating higher accumulation of finer particles, a negative value that the distribution was more on the coarse side, an effect of higher flow affecting the riverbed. The skewness therefore indicates the "energy level" of the deposition environment and the degree of the particle mixing (Sly 1978). There was little skewness in the distribution pattern at the centre and western side of site 10 and northern side of site 11; the distribution of particle size in these sediments was relatively symmetrical around the mean value.

W/D ratio and organic content

The wet to dry ratios (W/D) from sites 1 and 3 averaged from 2.11 to 3.08 (Table 2). The range was highest at site 3, near the middle of the inlet adjacent to the SCM pipeline. There was a greater depth gradient at this site. The water depth of the sites ranged from 0.5 m (site 1) to approximately 2.0 m (site 3).

Mean organic content was 8.6 to 12.1% (Table 2). Sediment organic content in Leschenault was higher than in Peel Inlet, comparable with some sites in Harvey Estuary, and clearly lower than in the Swan River. Distribution of sediment Al and Fe in these four estuaries followed the pattern of organic content. In Leschenault, concentrations were highest at site 1 and lowest at site 27, which was

Table 2. Physical and chemical properties of the sediments from Leschenault Inlet, Harvey Estuary, Peel Inlet and Swan-Canning Estuary.

Estuary	Site	W/D*		Organic matter (%)		CaCO$_3$ (%)	Al (%)	Fe (%)	Ca (%)
Leschenault Inlet	1	2.83	(2.79-3.97)	11.17	(9-8-15.2)	13.0	3.6	4.4	13.0
	3	3.08	(1.85-4.50)	12.08	(5.7-14.9)	8.0	3.4	4.0	2.5
	27	2.11	(1.72-3.41)	8.60	(3.9-15.6)	24.0	1.5	1.9	2.4
Harvey Estuary	1	4.88	(2.72-6.29)	17.72	(12.2-22.0)	9.0	6.0	3.8	2.9
	28	2.69	(2.20-3.56)	8.73	(1.0-11.9)	6.0	2.6	1.8	2.1
	29	3.55	(2.30-5.05)	10.84	(8.0-17.6)	35.0	4.2	2.6	14.4
	30	1.30	(1.28-1.58)	2.30	(1.0-3.5)	2.0	0.8	0.5	0.6
	31	2.21	(1.51-6.00)	5.38	(1.8-19.0)	3.0	1.0	0.6	1.0
	37	3.41	(1.73-6.25)	9.49	(3.0-18.4)	1.0	1.8	1.2	0.2
	P59	4.60	(3.14-5.65)	18.63	(11.7-22.0)	9.0	7.6	5.5	1.6
Peel Inlet	4	1.87	(1.47-2.11)	4.5	(1.4-6.3)	4.0	0.5	0.5	1.8
	5	1.55	(1.44-1.85)	3.1	(0.9-4.6)	1.0	0.2	0.2	0.2
	6	1.45	(1.33-1.95)	2.7	((0.6-4.9)	1.0	0.2	0.1	0.4
	7	1.65	(1.60-1.92)	6.0	(3.3-7.6)	20.0	1.4	1.2	8.2
	8	2.47	(1.71-3.59)	8.4	(4.5-14.5)	5.0	2.8	2.0	1.8
Swan-Canning Estuary	5	3.92	(2.27-5.57)	14.1	(8.6-20.6)	4.0	9.1	6.2	0.5
	9	5.00	(4.41-5.50)	19.2	(16.0-21.6)	5.0	9.3	7.0	0.7
	13	4.33	(3.61-5.40)	18.5	(14.6-19.9)	14.0	8.1	5.0	5.0
	16	4.17	(3.41-5.05)	19.5	(15.3-22.6)	7.0	9.7	5.2	1.7
	23A	4.67	(4.25-5.74)	19.2	(16.6-21.8)	15.0	6.4	5.8	4.7

*W/D: Wet to dry ratio by weight; range in parentheses

Table 3. Properties of surface sediments from Collie River.

Site	Depth (m)	W/D ratio	Total phosphorus (¯g g^{-1})
Collie 5 North	1.6	3.82	1106
Collie 5 South	2.7	3.24	881
Collie 5 Centre	2.7	1.84	221
Collie 10 West	4.1	3.46	666
Collie 10 East	2.0	4.37	856
Collie 10 Centre	4.1	4.76	1084
Collie 11 North	1.5	2.11	381
Collie 11 South	1.5	1.64	194
Collie 11 Centre	1.5	1.79	267
Collie 13	5.0	6.42	1102

apparently more affected by exchange of water between the inlet and ocean. Sediments from Leschenault Inlet showed similar trends to those of Peel Inlet and Harvey Estuary, where the concentration of iron and aluminium contents were correlated with % organic matter ($r^2 = 0.84$ and 0.86 for Al and Fe, respectively).

The central sites (sites 5 and 11) of the Collie River had lower W/D ratios than those on the north and south banks, although the ratio at the central site (site 10) remained high (Table 3). The W/D ratios at site 5 (north) and site 10 (east) were relatively high although the water was relatively shallow. Each of these sites was inside a bend in the river, where water flow is reduced and fine particles accumulate, whereas water velocity at the outside of bends discriminates against the settlement of fine particles. Only one sample was collected from site 13, upstream of the confluence with the Brunswick River where the river narrowed considerably.

Phosphorus forms

There were high variations in concentrations of sediment phosphorus between months, sites and estuaries (Table 4). The level of the total phosphorus in Leschenault Inlet was higher than in Peel Inlet ($p = 0.013$), but lower than in the Swan-Canning Estuary ($p = 0.002$). Although mean total P appeared low when compared with Harvey Estuary, it was not statistically significant ($p = 0.093$) at 95% confidence level. The low confidence level of the differences was partly attributable to the small site numbers in Leschenault Inlet, and the large between-site variations in Harvey Estuary.

Sediment total P in the Swan-Canning Estuary was significantly higher than in the Peel Inlet and Harvey Estuary ($p = 0.050$ and 0.005 respectively).

Organic phosphorus in the Leschenault sediments accounted for 19 to 31% of total P, with an average similar to Harvey Estuary (25%). This proportion was higher than in the Swan-Canning (19.6%). There was no significant difference in organic phosphorus content between Leschenault and Peel Inlet, and between Leschenault Inlet and Harvey Estuary. Organic phosphorus in Leschenault Inlet was significantly lower compared with the Swan-Canning Estuary ($p = 0.006$). Apatite phosphorus averaged about 37% of the total P in Leschenault sediments, the highest among these estuaries. This may reflect a strong marine influence, as apatite phosphorus can be 5 times higher in ocean sediments than in the Peel-Harvey (Lukatelich & McComb 1986). The concentration of apatite-P was higher in Leschenault than in Peel, but lower than in the Swan-Canning Estuary ($p = 0.036$ and $p = 0.020$, respectively). Non-apatite phosphorus averaged about 36% of total P in Leschenault Inlet, comparable with Peel Inlet (36.8%), but lower than in Harvey Estuary (46.1%) and Swan Canning Estuary (56.7%). The concentration of non-apatite P was also lower in Leschenault than in Harvey Estuary and the Swan Canning Estuary ($P = 0.032$ and 0.021 respectively).

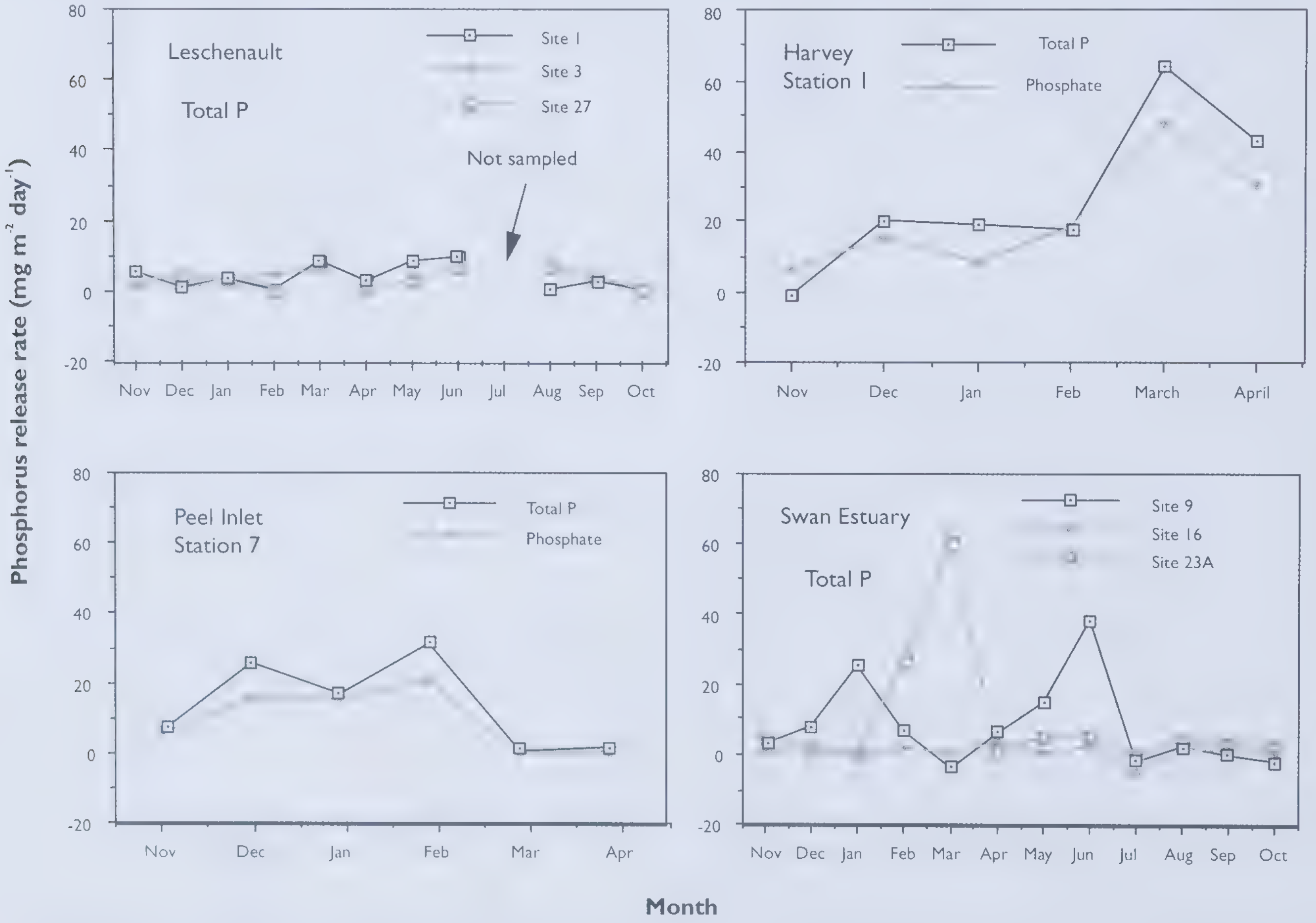

Figure 4. Sediment phosphorus release from intact cores collected from several estuaries south-western Australian. Sampling sites are shown in Fig.1.

Table 4. Forms of sediment phosphorus in Leschenault Inlet, Peel Inlet, Harvey Estuary and the Swan-Canning Estuarine System. Data range in brackets.

Estuaries	**Site**	**Total P** ($\mu g\,g^{-1}$)	**Organic P** ($\mu g\,g^{-1}$)	%	**Apatite P** ($\mu g\,g^{-1}$)	%	**Non-apatite P** ($\mu g\,g^{-1}$)	%
Leschenault	1	389 (283-379)	74 (39-151)	19.0	144 (55-98)	37.0	158 (57-202)	40.6
	3	313 (211-617)	97 (39-142)	31.0	81 (53-231)	25.9	110 (55-191)	35.1
	27	290 (200-420)	59 (26-97)	20.3	124 (30-218)	42.8	85 (23-216)	29.3
	Mean	**331**	**77**	**23.5**	**116**	**35.2**	**118**	**35.0**
Peel	4	227 (124-321)	62 (124-321)	27.3	56 (8-74)	24.6	95 (8-146)	41.8
	5	159 (107-242)	51(40-91)	32.1	37 (24-61)	23.2	58 (33-108)	36.5
	6	141 (96-217)	49 (27-84)	34.7	34 (15-52)	24.1	45 (28-88)	31.9
	7	217 (217-260)	60 (50-86)	27.6	73 (41-100)	33.6	73 (29-171)	33.6
	8	289 (213-431)	84 (55-181)	29.1	91 (54-150)	31.5	113 (50-201)	39.1
	Mean	**206**	**61**	**30.2**	**58**	**27.6**	**77**	**36.8**
Harvey	1	676 (386-888)	193 (40-91)	28.6	148 (13-198)	21.9	327 (187-390)	48.4
	28	400 (271-583)	100 (80-142)	25.0	107 (64-147)	26.8	177 (132-257)	44.2
	29	469 (441-575)	104 (46-145)	22.2	117 (86-142)	24.9	223 (159-281)	47.5
	30	180 (113-300)	59 (360-130)	32.8	38 (13-73)	21.1	73 (43-107)	40.6
	31	270 (142-797)	64 (30-189)	23.7	62 (32-159)	23.0	122 (56-395)	45.2
	37	477 (221-777)	105 (50-176)	22.0	120 (40-194)	25.2	213 (126-402)	44.7
	P59	545 (179-885)	113 (31-240)	20.7	156 (97-253)	28.6	283 (109-493)	51.9
	Mean	**431**	**105**	**25.0**	**107**	**24.5**	**203**	**46.1**
Swan-Canning	5	1013 (473-2136)	183 (20-648)	18.1	278 (84-1011)	27.4	548 (470-776)	54.1
	9	1689 (1489-3082)	174 (28-1067)	10.3	437 (177-1061)	25.9	1221 (514-1758)	72.3
	13	892 (566-1275)	164 (36457)	18.4	289 (201-441)	32.4	532 (314-944)	59.6
	14A	211 (126-328)	69 (33-101)	32.7	49 (20-83)	23.2	82 (51-123)	38.9
	16	696 (540-1019)	155 (47-236)	22.3	228 (104-330)	32.8	391 (217-737)	56.2
	23A	761 (530-1597)	122 (24-278)	16.0	258 (118-360)	33.9	448 (249-789)	58.9
	Mean	**877**	**145**	**19.6**	**257**	**29.3**	**537**	**56.7**

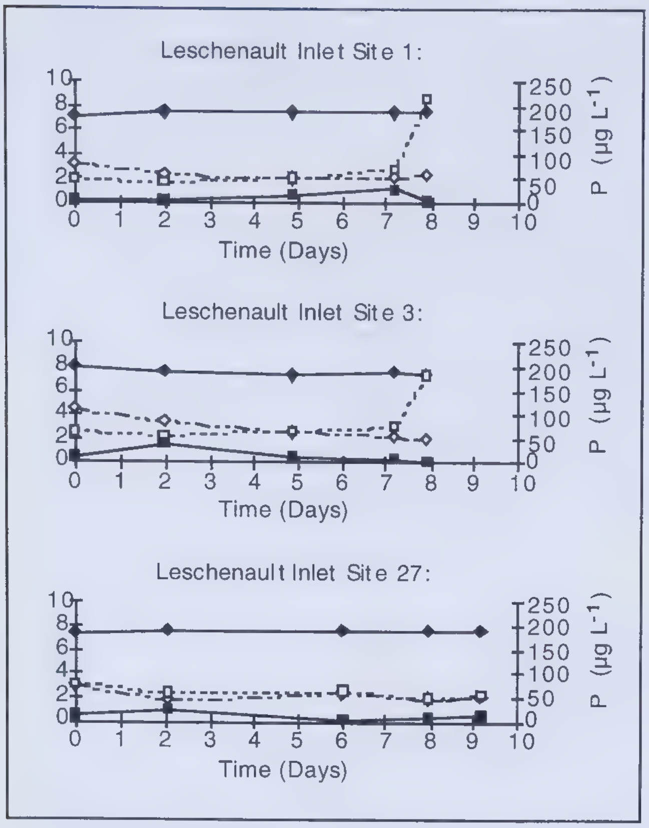

Figure 5. Phosphorus (SRP and TP) release and related pH and DO concentrations (mgL^{-1}) in intact cores collected in March 1990 from Leschenault Inlet. Site 1; Site 3; Site 27. —◆— pH; - - ◇ - - - DO; —■— SRP; - - -□- - - TP.

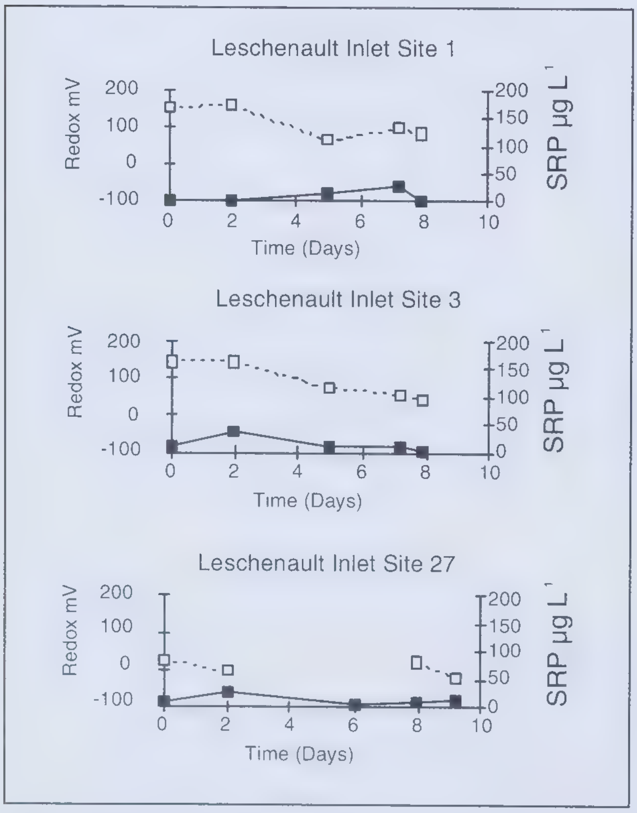

Figure 6. Phosphate (SRP) release and redox potential in intact cores collected in March 1990 from Leschenault Inlet. Site 1; Site 3; Site 27. - - - -□ - - - Redox; —■— SRP.

Potential for phosphorus release

The laboratory incubations of intact cores suggested that the potential for sediment phosphorus release was relatively small in Leschenault Inlet (Fig 4). In some cases phosphate concentrations in the water column fell during incubation. This occurred in the sediment cores from Site 1 and Site 27 in February to March. Rates of phosphate and total phosphorus release were low in most months compared with other estuaries.

There was little change in water column pH from all three sites in Leschenault Inlet, but DO and redox potential decreased with time (Figs 5, 6). There was no oxygen depletion during incubation, as there was in organic-rich sediments, such as those from Harvey Estuary. Paired cores from Harvey Estuary in the same period showed significant oxygen depletion during incubation. Conditions developed in the water column may favour nutrient release from sediment, but changes in water column concentrations were relatively small. The possibility remains that phosphate in the water column may have been in part transferred to the particulate phase, for example, attached to particle surfaces or taken up by phytoplankton and other microorganisms. The increase in total phosphorus at the end of incubation suggests that such activity could have been involved in altering phosphate concentrations in the water column.

Sediment release rates for phosphate were –15.8 (*i.e.* the water concentrations fell) to 5.6 mg m^{-2} d^{-1} in Leschenault Inlet (Table 5), and the calculated annual average would be -0.11 mg m^{-2} d^{-1}. This is extremely low compared with the estimated annual rate for Harvey Estuary during 1982-1990 (Table 5). Table 6 also shows that phosphate release from the sediments studied is always coupled with ammonium release, though this information is not directly available for Leschenault Inlet.

Interrelations between components

There was a significant correlation between W/D ratio and total phosphorus in Collie River sediments (Fig 7). Similar correlations exist in many other estuaries in south-western Australia (Fig 8), despite difference in trophic status and sediment phosphorus concentrations. The slope of the relationship, however, may differ between systems according to sediment properties and the degree of nutrient enrichment (Hill *et al.* 1991; McComb *et al.* 1998).

W/D ratio was also correlated with the proportion of particles less than 75 µm in Leschenault, Peel-Harvey and Swan-Canning estuaries ($r^2 = 0.74$, $p < 0.01$). There was no correlation between water depth and the other parameters measured in Collie River. This may suggest that water flow, rather than local morphology, is the dominant factor in the distribution of sediment components.

Surface sediments from Leschenault Inlet had a large proportion of fine material, with a particle size finer than in the Peel-Harvey Estuary. Consistent with this, organic enrichment of surface sediment was relatively high. It was higher than in Peel Inlet, comparable with part of Harvey Estuary, but lower than in central Harvey Estuary and the Swan-Canning Estuary.

This paper focused on the redox-related P release,

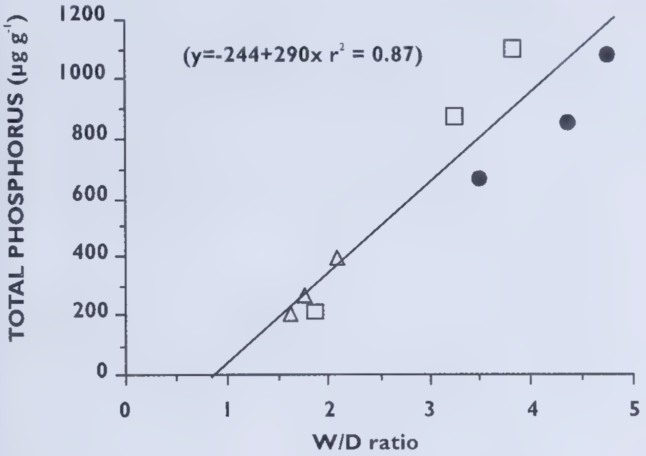

Figure 7. W/D ratio and total phosphorus content in sediments from Collie River. □ Site 5; ● Site 10; △ Site 11.

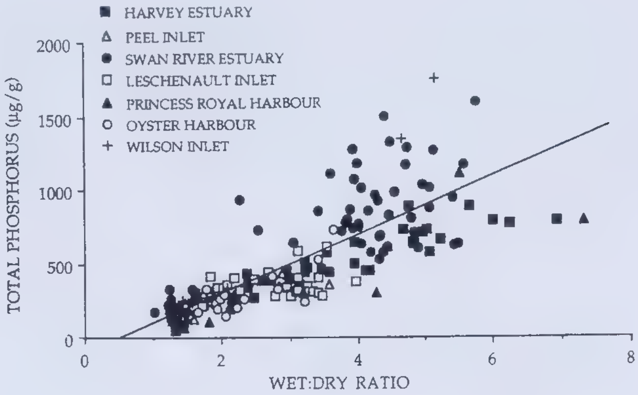

Figure 8. W/D ratio and total phosphorus concentrations in sediments from estuaries of south-west Australia. (y=105.29 + 193.78x; r=0.65).

which was usually driven by bacterial activity and triggered by favorable conditions including high respirable C. Several factors are usually associated with this type of P release, mainly a) the level of organic respiratory C; b) the composition of the sediment P form, and c) their absolute amounts. The organic content in Leschenault Inlet was higher than in Peel Inlet and similar to that of the Harvey Estuary. Sediment oxygen demand associated with the degradability of organic matter was similar to those in the Peel Inlet and Swan-Canning Estuary, though it was lower compared with those in Harvey Estuary (Qiu & McComb unpublished data). Therefore it is difficult to interpret the different P release rates between estuaries by the amount and the nature of organic matter alone. On the other hand, there was no clear indication that the level of 'absolute amount' of any sediment P forms was predominantly higher or lower in Leschenault, which may be responsible for the difference in P release. The proportion of apatite-P to total P, however, appears to be consistent with the P release data. The Leschenault sediments contain a substantial proportion of apatite P, distinctly higher than in Peel, Harvey and Swan-Canning.

At least in part for this reason, the rate of P sediment release remained low in Leschenault Inlet compared with the other estuaries. This low P release may be also related to the overall effects of other factors, such as the relatively low amount of sediment P forms, though this was not strongly supported by the limited sediment data. Likewise, the field conditions should not be neglected, as this type of P release is usually triggered under favorable environmental conditions, such as an increased water, which stimulates microbial development near the sediment-water interface.

Table 5. Phosphate release rate (mg m^{-2} day^{-1}) over 10 days' incubation from Leschenault Inlet sediments, between November 1988 and October 1989.

Station	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
1	1.5	3.6	1.6	-5.2	-0.2	-15.8	5.3	3.6	*	3.4	1.0	0.7
3	5.2	1.2	2.3	1.5	-0.2	-15.4	-	-	*	-	-	-
27	-0.1	2.4	2.1	0.3	-	0.8	1.6	1.6	*	5.6	1.8	0.3

*Samples were not collected because of poor weather conditions.

Table 6. Phosphate and ammonium release rates (± se) of sediments from Station 1 in Harvey Estuary.

	Harvey Estuary		Peel Inlet	
Year	Phosphate (mg m^{-2} day^{-1})	Ammonium (mg m^{-2} day^{-1})	Phosphate (mg m^{-2} day^{-1})	Ammonium (mg m^{-2} day^{-1})
1982	24.3 ± 9.6	-	-	-
1983	28.4 ± 4.4	98.3 ± 13.3	-	-
1984	20.6 ± 3.3	194.9 ± 33.8	5.2 ± 2.1	102.4 ± 26.4
1985	19.8 ± 4.0	216.2 ± 51.5	4.5 ± 0.9	128.2 ± 33.0
1986	20.5 ± 4.6	212.5 ± 40.5	4.9 ± 1.7	75.8 ± 16.3
1987	13.1 ± 5.5	202.2 ± 49.0	2.7 ± 1.2	86.2 ± 11.7
1988	5.2 ± 2.4	75.8 ± 14.1	3.0 ± 3.5	63.5 ± 15.2
1989	14.3 ± 4.4	252.8 ± 67.3	8.5 ± 1.7	252.8 ± 67.3
1990	16.7 ± 5.4	-	7.2 ± 2.8	-

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Ecological significance of freshwater seeps along the western shore of the Leschenault Inlet estuary

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Abstract

The natural seepage lines of the Leschenault Peninsula are expressions of the topography and stratigraphy, which act as sink and conduits for discharging groundwater. The drainage of the aquifer follows the lowest point in the landscape, and continues for some time after winter rainfall has ceased. Freshwater seepage sites are important in the first instance for peripheral estuarine vegetation that exploit these zones of lower salinity in an area of otherwise saline high tidal flats. Secondly, freshwater sources in the hot dry summer environment may be exploited by avifauna, particularly as no permanent freshwater sources exist on the Peninsula.

Keywords: Leschenault Inlet, south-western Australia, estuary, freshwater seepage, peripheral vegetation.

Introduction

The Leschenault Peninsula separates the shallow saline water of a lagoon, the Leschenault Inlet, from the Indian Ocean, and consists of vegetated and mobile dunes. There are no streams or channels on the Peninsula, and drainage is internal. Winter rainfall recharges the groundwater system of the peninsula with a resultant rise in groundwater level. During the ensuing spring and early summer, the elevated water table discharges to the inlet and the ocean through freshwater seepage. This seepage forms important sites of mixing between freshwater and saline water which influences the occurrence and distribution of native shore vegetation, and combined with the natural setting and food resources of the Leschenault Inlet, provides important habitat for both permanent and migratory birds.

The objective of this paper is to describe the geomorphic, stratigraphic and hydrologic setting of the Leschenault Peninsula barrier dunes in their relationship to the western shore of the Leschenault Inlet estuary to explain the localised sites of freshwater seepage along this western shore, and to describe some of its ecological effects. The approach of this study was one of using landscape ecology which attempts to integrate data from a variety of disciplines (in this case geomorphology, stratigraphy, hydrology, vegetation, and avifauna) to provide an understanding of ecological processes and patterns. The value of such an approach is that it provides integrated multi-disciplinary information for management.

Regional setting

The Leschenault Peninsula is a linear barrier dune system, some 12 km long and 0.5-1.5 km wide (Fig 1), and is located along the south-western Australian coast in the Leschenault-Preston Coastal Sector (Searle & Semeniuk 1985; Semeniuk 1985). Geomorphologically, this coastal terrain is referred to the Quindalup Dunes, the system of white to cream coastal dune sands distributed along the Western Australian coast from Geographe Bay to Dongara (McArthur & Bettenay 1960; Semeniuk et al 1989). The study area has an annual rainfall of *ca* 880 mm, and an annual evaporation of *ca* 1980 mm (Anon 1975; Semeniuk & Meagher 1981a). Tides in this region are microtidal, with a maximum range of 0.9 m, and a prevailing range of 0.5m.

Stratigraphy of Leschenault Peninsula

The Leschenault Peninsula is comprised of up to 40 m of Holocene dune sand forming an extensive shore-parallel prism and referred to the Safety Bay Sand, which is mainly quartz and carbonate fine to medium sand of coastal aeolian origin (Semeniuk 1983). The Safety Bay Sand is underlain by a ribbon, some 6 m thick, of Leschenault Formation, an estuarine sedimentary unit composed of mud, shelly mud, muddy sand, and grey sand. This formation underlies and interfingers with the Safety Bay Sand on the eastern side of the barrier. Here, the stratigraphic relationship between the two formations is complex for the following reasons (Semeniuk 2000):

- the present shore face between the dune and the estuary is comprised of dune fingers (the fronts of parabolic dunes) extending into the muddy environments of the estuary, with muddy sediments accumulating between the dune promontories, generating a laterally alternating system of dune sand bodies overlying muddy sand sequences and mud sequences;
- the Leschenault Formation varies lithologically laterally and down-depth from muds to muddy sand to sand, with the various lithologies developed in lenses, ribbons and sheets, and interfingering; and
- the present contact between dune sand and the muddy sediment of the estuary along the eastern side of the Peninsula is situated at about the high tide mark, however, earlier in the Holocene, with sea-levels higher than at present (Semeniuk 1985), the contact locally could be up to 2 m or more above the present high tide level.

On the east side of the barrier, the Safety Bay Sand is fairly consistent in its lithology throughout its length and depth, while the Leschenault Formation is more variable, with mud, or muddy sand, or sand developed at the contact between it and the Safety Bay Sand, and the stratigraphic contact developed at the level of the present high water mark or higher. All of these factors have implications for

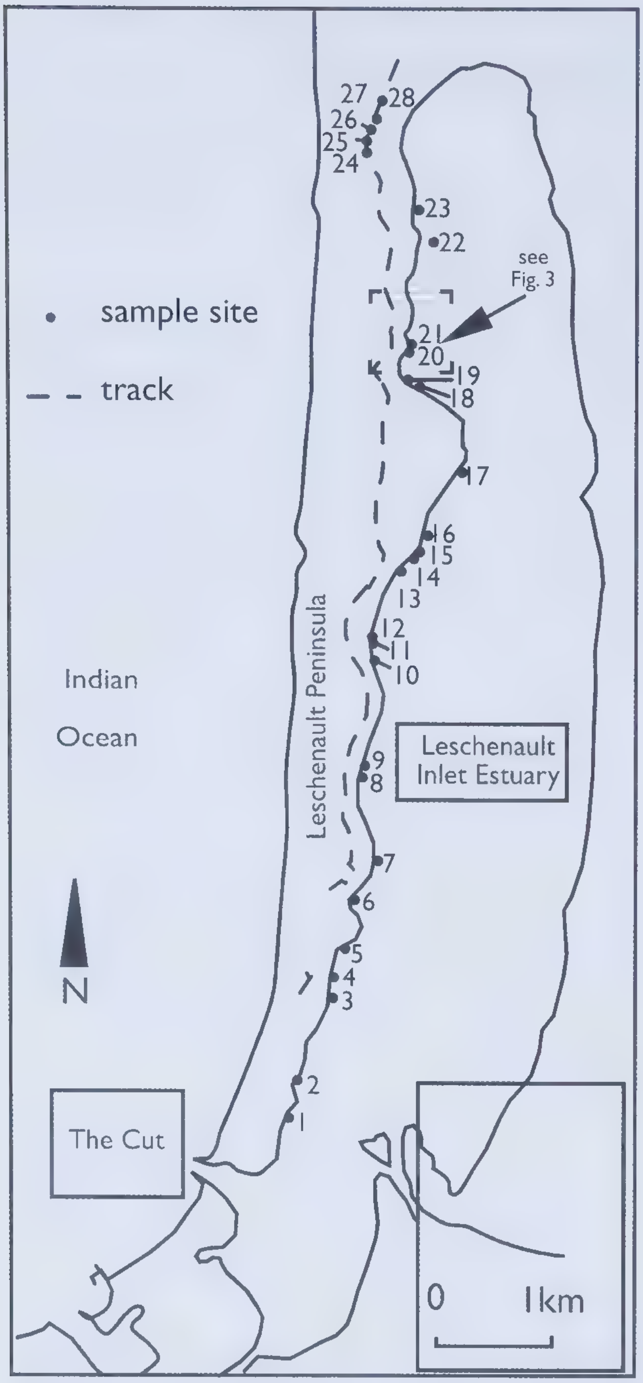

Figure 1. Location of sampling sites along eastern shore of the Leschenault Peninsula.

the hydrological dynamics along the Leschenault Peninsula eastern shore.

Hydrology

As a barrier dune complex, Leschenault Peninsula separates the marine waters of the Indian Ocean to the west from the marine to estuarine waters of Leschenault Inlet to the east (Fig 1). Under the Peninsula, within the Safety Bay Sand, there is a prism of freshwater, and a saline/freshwater interface descending steeply at depth on both the ocean and estuarine side of the barrier (Semeniuk & Meagher 1981b). In essence, this hydrological situation is an analogue of a freshwater lens in an oceanic island setting, where a core of freshwater is surrounded by marine water. The groundwater table under the Peninsula is not planar, but forms an asymmetrical low mound, rising up to 0.8 m above sea-level towards the ocean side of the Peninsula, and located *ca* 0.2 m above sea-level towards the inlet side of the Peninsula (Fig 2; after Semeniuk & Meagher 1981b).

Hydrologic dynamics

In response to seasonal rainfall, the water table under the barrier dune fluctuates vertically 0.3-0.5 m, locally raising the water table to 1 m above MSL (Semeniuk & Meagher 1981b). At times of maximum water table elevations, when there may be a 0.5-1.0 m hydraulic head difference between the freshwater water table and the surface of the marine/estuarine water bodies, there is freshwater discharge (expressed as surface seepage) into lowlands and into the adjoining tidal zones. On the eastern side of the Peninsula, where groundwater hydrodynamics are important to the subject matter of this paper, the water table generally slopes down to the estuary margin. Here there are three situations that determine the style and amount of freshwater discharge:

1. dunes are truncated by estuarine coastal erosion forming small sand cliffs 1-3 m high; winter-recharged groundwater stored in the barrier discharges into the inlet along this estuary shore;
2. large fingers of dune sand (encroaching parabolic dunes) extend into the estuary; a low mound of freshwater occurs under such fingers, and these form reservoirs to discharge locally into the Inlet environment; and
3. a shallowly buried sheet of mud slopes towards the estuary; this acts as an aquatard and water discharging vertically under a high winter hydraulic head is laterally diverted, and discharges along the estuary shore.

At times of low tides, the hydraulic head between the groundwater under the barrier dunes and the adjoining Inlet is relatively large, and the discharge outlined in the three situations above is exacerbated. Discharge along the estuarine shore-face during these times of low tide are best developed during the winter/summer transition, for the following reasons: 1. mean sea-level is falling from a winter high to a summer low (Semeniuk & Meagher 1981b); 2. winter watertable levels are at their maximum, and hence the hydraulic head differences between the freshwater aquifer and the estuary are most marked; and 3. this time generally is a period of equinoctial tides, further increasing the difference in the hydraulic head.

Methods

The identification of natural seepage lines from the Leschenault Peninsula into the Leschenault Inlet was undertaken using three environmental indicators:

1. landform/vegetation units; 2. salinity of surface water and groundwater; and 3. occurrence of avifauna.

A study of the landscape features of landform and vegetation was undertaken along the full length of the Peninsula as the first step to more narrowly define possible seepage points. Interpretation of dune morphology and vegetation units along the eastern shore of the Leschenault

Peninsula provided potential freshwater seepage sites for more detailed field investigation. Stereoscopic aerial photographic interpretation (SAPI) of the landform characteristics and associated vegetation units was undertaken to determine those landform elements most likely to be associated with freshwater seepage. Four major landform elements were investigated:

a) interdunal swales oriented perpendicular, and close to, the inlet edge;

b) sharp interdunal contact areas between converging dunes, close to, or at the inlet edge;

c) apical cusp (or "toe") of dunes close to, or at the inlet edge; and

d) localised elongate depressions, particularly those oriented perpendicular to the inlet edge.

A field survey was undertaken to ground-truth landform units identified by SAPI, to document vegetation, to collect surface and groundwater water samples, and to observe avifauna in relationship to any identified freshwater seepage. To identify and ground-truth potential seepage sites, a complete north-south traverse of the inlet/peninsula interface was undertaken, with selected sites revisited for observing avifauna and sampling for water. The ground-truthing of landform units was undertaken to verify that the units defined by SAPI were actual changes in topography and vegetation cover, and not an artifact of changes in aerial photographic tones.

Vegetation was surveyed to determine its relation to surrounding landforms, and particularly in relation to areas where the "wetness" of the estuarine environment continued up-slope beyond the intertidal range, indicating freshwater seepage. The survey of the vegetation was a broad identification of major units, rather than quantitative quadrat survey. The survey concentrated on the structural vegetation units of 'rushland' and 'sedgeland' along the land/estuary interface to identify areas of wetland vegetation type continuing beyond the inlet edge.

Once potential seepage points were identified using the landform and vegetation indicators, more detailed surface water and shallow groundwater sampling was undertaken. Twenty-eight such sites were identified (Fig 1). At each potential seepage site the vegetation was traced up-slope to the landward extreme of the "wetness", which was usually at the edge of higher relief dunes. The site of potential freshwater seepage represents areas of lower salinity within a context of a saline upper tidal flat. At each locality, a surface water or groundwater sample was collected. Where this interface was more than 100 m from the inlet edge (*i.e.* the "area of wetness" was extensive or linear perpendicular to the inlet edge between converging dunes), a second, or third water sample was collected closer to the inlet. Each water sample was collected from shallow groundwater or from surface water pools greater than 10 cm below the surface of the water, where possible, to account for any possible fresh water perched on top of potentially a more saline base water. Site 21 was revisited for mapping and water sampling in March 1997.

Observations on the avifauna were undertaken on two occasions following Storr (1991) and Johnstone & Storr (1998): firstly, during the initial traverse of the inlet/peninsula interface and water sampling, and on a second field visit to collect further water samples and to specifically observe bird behaviour in relation to the seepage areas in early summer. Birds were observed for potential usage of freshwater seepage along the entire length of the Peninsula, though effort was concentrated on areas already identified by the landform analysis as the main seepage sites. Field studies were carried out in spring and early summer after the majority of the year's rainfall had ceased, and maximum seepage of groundwater would be expected from the elevated groundwater levels on the Peninsula.

Water samples were determined for salt content in the field with a refractometer, and confirmed in the laboratory using an electrical salinometer.

Results

Broad seepage front

The length of the edge of the dune terrain of the Leschenault Peninsula generally abuts a narrow to broad high-tidal flat. Groundwater residing within the dune sand

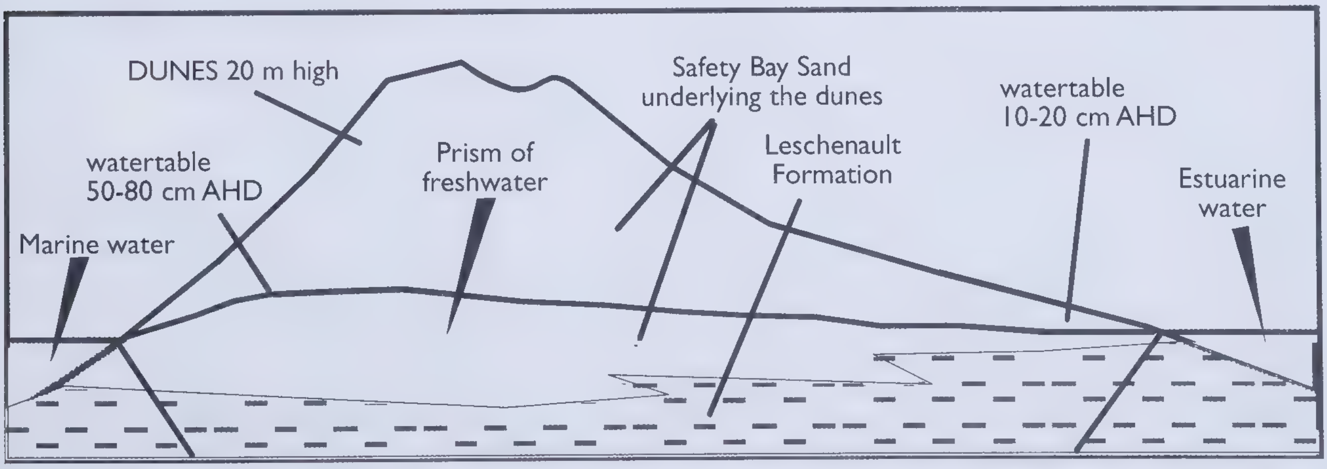

Figure 2. Idealised cross-section of the Leschenault Peninsula showing stratigraphic and hydrologic features (after Semeniuk & Meagher 1981b). Maps showing terrain, study sites, seepage sites, and salinity values of sampling sites around the dune projection of Site 21 in March 1997.

Table 1. Salinity of sampling sites 1 part per thousand = 1000 mg L^{-1}. Values are mean and number of samples (n).

Sampling Site	Total Dissolved Solids ‰	n
1	2.2*	4#
2	22.6	2
3	8.5	3
4	13.5	2
5	3.8+	2
6	1.4*	2
7	17.1	1
8	2.0*	4
9	17.6	2
10	3.8+	1
11	14.7	1
12	3.2+	2
13	17	1
14	2.95+	2
15	3.2+	2
16	20	1
17	3.2+	1
17	4.9+	1
19	4.9+	1
20	1.6*	2
21	0.4*	1
22	19	1
23	4.0+	1
24	10.5	1
25	1.6*	1
26	4.5+	1
27	3.2+	1
28	30	1

* < 3 000 mg/L^{-1}TDS

+ 3 000 - 6,000 mg/L^{-1}TDS

# One value deleted, as considered atypical.

is freshwater (Semeniuk & Meagher 1981), and that under the tidal flats is saline to hypersaline. Vegetation on the dunes comprises a mix of shallow to deep-rooted, phreatic and vadose freshwater dependent terrestrial vegetation, while that on the tidal flats comprises halophytes. The interface between the two vegetation systems is a ubiquitous shore-parallel seepage of freshwater. Across this interface, groundwater salinity changes in the direction from estuary to landward, from saline to brackish to fresh (Table 1; Fig 3). Hence, it is a zone of mixing of freshwater and saline water, and is inhabited by a fringe of *Juncus kraussii* closed rushland (*Juncetum kraussii* association of Cresswell & Bridgewater 1998), which is euryhaline in its habitat range).

Discrete seepage sites

In addition to the laterally extensive seepage front, there are numerous discrete seepage points where there is a more pronounced localised freshwater discharge into the saline tidal flats. Landscape analysis of landform and vegetation using aerial photographic interpretation identified 28 such seepage sites, mostly covered or surrounded by *Juncus kraussii* closed rushland. Twenty four of these seepage sites contained some open standing water (*i.e.* windows to the water table) at some part of their distribution, ranging from very small pools directly on the dry dune/wet zone interface (less than 1 m^2) to extensive ephemeral wetlands (over 500 m^2) occurring as shallow pools within the high-tidal flats along the inlet edge. A list of seepage sites and notes on the surrounding vegetation are presented in Tables 2 and 3.

Along the northern section of the Peninsula, the landform abutting the Inlet is mostly undulating plain, and the peripheral vegetation to the seepage sites is dominated by *Eucalyptus gomphocephala* open forest and *Melaleuca rhaphiophylla* low open forest with *Lepidosperma gladiatum* and *Juncus kraussii* closed rushland understorey. Along the southern section of the Peninsula, the dominant landform is parabolic dune-fields, and the peripheral vegetation to the seepage sites is *Juncus kraussii* closed rushland with no overstorey. The slightly undulating landform in the north provides a gentler gradient between the seepage areas and the surrounding terrain yielding a greater areal extent of the wet zone and a mixture of species present at the seepage points. In the south, the distinct interface between the wet zone and the parabolic dunes does not favour a mixing of the vegetation between the habitats.

Salinity of seepage sites

The salinity of the open Inlet water is generally 35 000 ppm, and the groundwater of the tidal flats is generally in excess of 50 000 ppm. Groundwater salinity within upper tidal flat or mid tidal flat settings in the range < 1 000 ppm, up to 6 000 ppm is strong evidence for freshwater dilution of the generally saline estuarine environment, and hence evidence for freshwater discharge.

At the 28 potential seepage sites on the first field visit in September 1986, water was collected from 34 sampling points for determination of salinity. Where the area of wetness at the site was extensive, two or more samples were collected. Further samples were taken later in the summer (November 1986) where standing water remained. Where two samples were taken at different times from the same sampling point the average of the two readings was used to characterise the sampling point.

The sites were then assigned into salinity classes according to Hammer (1986) as follows: Less than 1 000 mgL^{-1} = fresh; 1 000–3 000 mgL^{-1} = subhaline; 3 000–20 000 mgL^{-1} = hyposaline; and 20 000–50 000 mgL^{-1} = mesohaline.

Using this classification, of the 34 sampling points only one was fresh, seven were subhaline, twenty-four were hyposaline and two were mesohaline. At all times, the salinity of the open estuarine waters was near seawater. The average salinity for each site was calculated as the mean of all samples taken at that site, which is presented in Table 2 (multiple sampling).

The salinity data show that the seepage sites have fresh to brackish groundwater or surface water, and where transects have been established, the salinity changes up-slope from saline estuarine and tidal flat groundwater to freshwater at the point of freshwater seepage. Due to mixing with the surrounding saline environment it would not be expected that salinity readings would remain below 1 000 mg L^{-1} at seepage sites. Therefore, a threshold of 3000 mg L^{-1} is adopted here to identify freshwater seepage. Along the dune barrier, there are six sites with average salinities below 3,000 mg L^{-1} identified as significant freshwater seepage sites.

Table 2. Total dissolved solids measured at sampling site transects 1, 2, 3, 4 and 8 with description of location and surrounding vegetation (see Fig 1 for site locations). A, B, C, D refers to multiple sampling along transect from inlet edge to landwards.

Site	Total Dissolved Solids (‰) 8.9.86	14.11.86	Location	Vegetation
1(A)	ns	35	Inlet water	
1(B)	ns	3.84	Beach seepage 1 m from inlet	*Cynodon dactylon* closed herbland
1(C)	8.4	2.6	Small open pool 5-10 m from inlet	*Juncus kraussii* closed rushland
1(D)	1.8	0.63	Sedgeland 50 m from inlet	*Juncus kraussii/ Baumea articulata* closed sedgeland.
2(A)	ns	36	"Billabong" 1 m from inlet	*Sarcocornia quinqueflora* closed herbland
2(B)	ns	9.2	Small open pool 50 m from inlet	*Juncus kraussii* closed rushland
3(A)		35	Inlet water	
3(B)	12.6	ns	Small open pool 10 m from inlet	*Sarcocornia quinqueflora* closed herbland
3(C)	4.6	8.3	Sedgeland 20 m from inlet	*Juncus kraussii/ Typha orientalis* closed sedgeland
4(A)	16.5	ns	Small open pool 10 m from inlet	*Typha orientalis* closed sedgeland
4(B)	10.6	ns	Rushland 100 m from inlet	*Juncus kraussii* closed rushland
8(A)		35	Inlet water	
8(B)	2.25	3.33	Open rushland 5 m from inlet, east	*Juncus kraussii* open rushland side of road
8(C)	0.99	1.53	Small open pool, 15 m from inlet, west side of road	*Juncus kraussii* closed rushland

ns = not sampled.

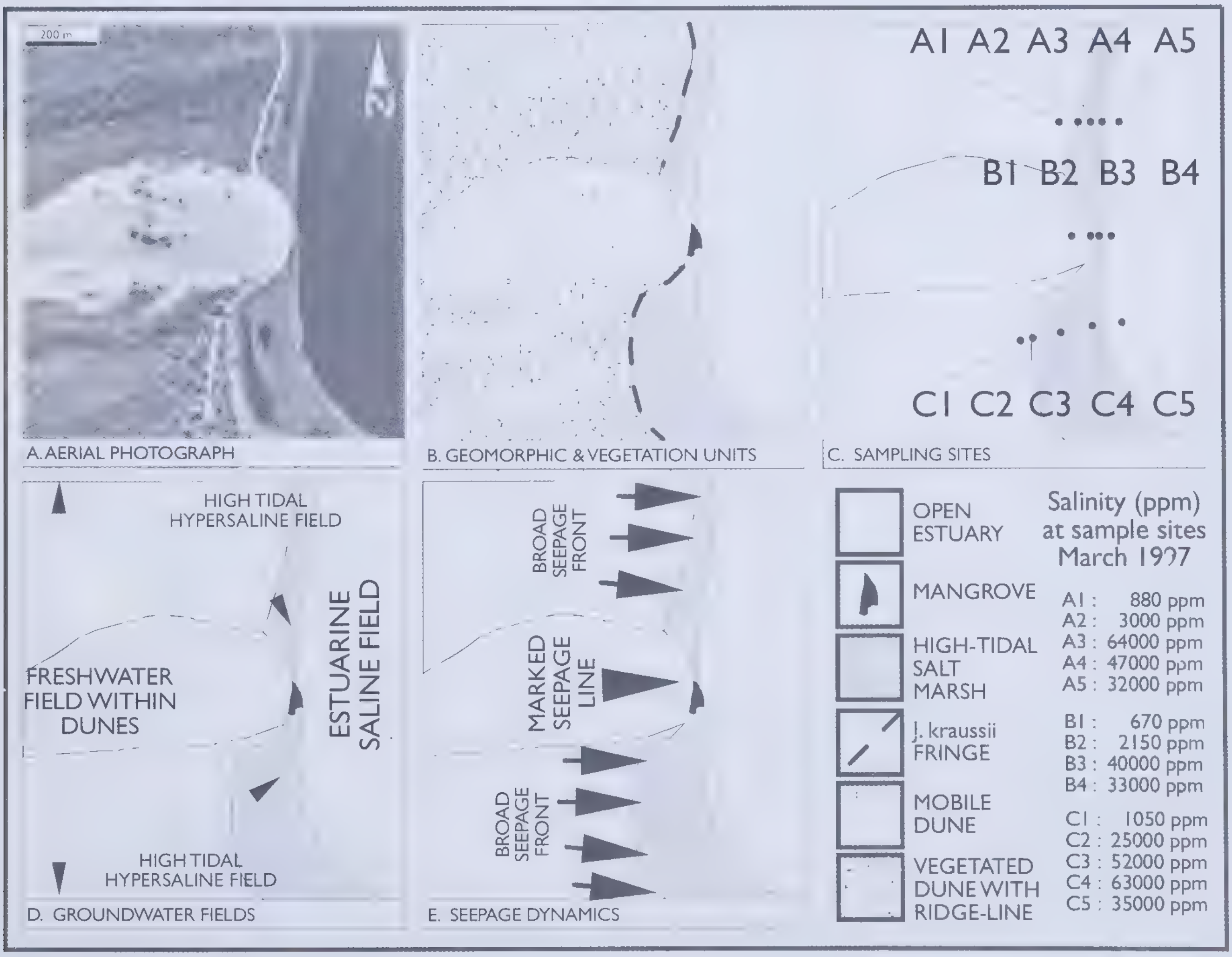

Figure 3. Maps showing terrain, study sites, seepage sites, and salinity values of sampling sites around the dune projection of Site 21 in March 1997.

Ten sites had average salinities between 3 000 and 6 000 mg L^{-1}, which may reflect minor seepage points having a diluting effect on the estuarine waters (Fig 4).

Site 21 is one of the best locations to study salinity changes induced by freshwater seepage into a saline groundwater environment (Fig 3). Here, a finger of dune sand is encroaching onto the high-tidal flat of the estuary. Fresh groundwater residing in the dune sand body forms an intrusive freshwater projection into the tidal flat. There

Table 3. Total dissolved solids measured at single sampling sites, with description of location and surrounding vegetation (see Fig 1 for site location)

	Total Dissolved Solids (‰)			
Site	**8.9.86**	**14.11.86**	**Location**	**Vegetation**
5	6.75	0.8	Rushland 100 m from inlet	*Juncus kraussii* closed rushland
6	1.35	1.44	Sedgeland 100 m from inlet	*Juncus kraussii*/ *Typha orientalis* closed sedgeland
7	17.1	ns	Small open pool 5 m from inlet	*Juncus kraussii* closed rushland
9	33	2.25	Small open pool, 20 m from inlet, west side of road	*Juncus kraussii* open rushland
10	3.8	ns	Small open pool, 5 m from inlet, east side of road	*Juncus kraussii* open rushland
11	14.7	ns	Small open pool, 10 m from inlet, east side of road	*Juncus kraussii* closed rushland
12	2.0	4.5	Small open pool, 30 m from inlet, west side of road	*Eucalyptus gomphocephala* open woodland
13	17	ns	Open water in closed rushland, 20 m from inlet, east side of road	*Juncus kraussii* closed rushland
14	3.3	2.6	Small open pool, 10 m from inlet (opposite .. line)	*Eucalyptus gomphocephala* open forest
15	2.5	3.87	Small open pool, 20 m from inlet	*Juncus kraussii* closed rushland
16	20	ns	Small open pool, 3 m from inlet	*Juncus kraussii* closed rushland
17	3.2	ns	Small open pool, 10 m from inlet	*Juncus kraussii* closed rushland
18	4.9	ns	Small open pool, 40 m from inlet	*Eucalyptus gomphocephala* open forest with *Lepidosperma gladiatum*
19	4.9	ns	Small open pool, 45 m from inlet	*Eucalyptus gomphocephala* open forest with *Lepidosperma gladiatum*
20	1.6	1.53	Small drainage rut, 20 m from inlet, west side of road	*Juncus kraussii* closed rushland
21	0.4	ns	Open water, 4 m from inlet	*Avicennia marina* closed scrub.
22	19	ns	Small open pool, 25 m from inlet	*Juncus kraussii* closed rushland / *Sarcocornia quinqueflora* closed herbland
23	4	ns	Small open pool, 100 m from inlet, 10 m east of road	*Melaleuca rhaphiophylla* low open forest / *Juncus kraussii* closed rushland
24	10.5	ns	Small open pool, 100 m from inlet, east side of road	*Melaleuca rhaphiophylla* low open forest
25	1.5	ns	Small open pool, 80 m from inlet, east side of road	*Melaleuca rhaphiophylla* low open forest
26	4.5	ns	Small open pool, 80 m from inlet, east side of road	*Melaleuca rhaphiophylla* low open forest
27	3.2	ns	Small open pool, 80 m from inlet, east side of road	*Eucalyptus gomphocephala* open forest / *Juncus kraussii* - *Lepidosperma gladiatum* open sedgeland
28	30	ns	Small open pool, 100 m from inlet, east side of road	*Eucalyptus gomphocephala* open forest

ns = not sampled.

is a steep hydraulic gradient between the fresh groundwater under the dune and the tidal flat, with brackish water in the zone of mixing along discharge/ seepage zone.

Vegetation

The saltmarsh and halophytic vegetation associated with the seepage sites are (Tables 2 & 3):

- the fringe of *Juncus kraussii* along the interface between the dunes and the saltmarsh;
- forests of *Melaleuca rhaphiophylla* along the upper part of the high-tidal shore;
- scrub of mangrove *Avicennia marina* at the tip of a dune advancing into the estuary;
- mosaics and fringes of *Lepidosperma gladiatum*; and
- occurrences of *Eucalyptus gomphocephala* along the shore in interdune areas.

Occurrences of these vegetation types at the various sites, together with the salinity of the groundwater and any surface water at the seepage site are described in Tables 2 & 3.

Avifauna

During the surveys, white-faced herons (*Ardea novaehollandiae*) and Australian shelduck (*Tadorna tadornoides*) were sighted consistently in the vicinity of the freshwater seeps. There also were large mixed groups of waders, cormorants, gulls and pelicans near several different seepage sites during both visits, including marsh sandpiper (*Tringa stagnatilis*), greenshank (*Tringa nebularia*), red-necked stint (*Calidris ruficollis*), Australian pelican (*Pelecanus conspicillatus*), crested tern (*Sterna bergii*), silver gull (*Larus novaehollandiae*), and great egret (*Egretta alba*).

During the first survey, however, conditions were windy and it was assumed that birds aggregated near seepage sites more for shelter from the wind, than for usage of freshwater. Also, heavy rainfall prior to the first field survey had resulted in freshwater being freely available over much of the low-lying terrain. Consequently, birds were widely dispersed over much of the area, and there was no need for birds to remain near seepage sites. The field survey thus showed no exclusive use of seepage areas by large numbers of birds. On the second field survey, high barometric pressure and low tide resulted in very low water level in the Inlet. Consequently, with the exposure of previously unavailable mudflats, most birds were away from the near-shore and feeding on the mudflats. Strong winds also affected bird behaviour with many species absent from the Inlet and near-shore, while many others found to be sheltering in the embayments. From this perspective, the information on avifauna collected during the two survey periods in relation to their use of freshwater seepage zones overall was inconclusive.

However, there were occurrences of single white-faced herons on ten of the small open pools associated with freshwater seepage, demonstrating some use of freshwater-influenced resources. Other white-faced herons were noted feeding in the estuary and saltmarshes. This species appeared to favour the sedgelands surrounding the small pools, presumably for protective cover, while feeding took place over the entire range of shallow waters in their immediate vicinity. Additionally, two breeding pairs of Australian shelduck were observed close to freshwater seepage points during September/October. Australian shelduck require freshwater bodies or estuaries and saline water bodies adjacent to freshwater sources, with nesting taking place in hollow trees, on the ground, in sandbanks,

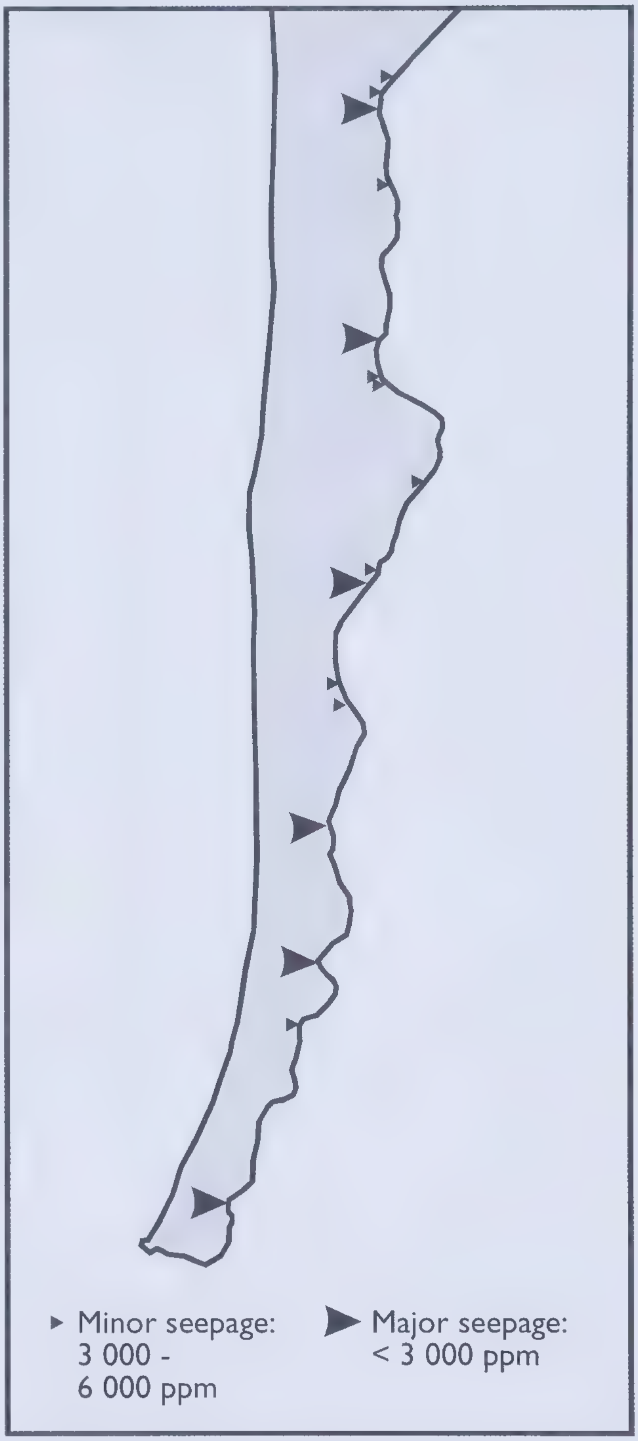
▸ Minor seepage: 3 000 - 6 000 ppm
➤ Major seepage: < 3 000 ppm

Figure 4. Map showing location of major and minor seepage sites.

and holes in limestone (Johnstone & Storr 1998). The presence of breeding pairs would indicate the reliability of the freshwater seepages.

Discussion

The combination of several environmental indicators within a landscape ecological approach provides a useful framework for understanding the natural processes operating at the landscape scale. In this context, the study of the landform, vegetation, water quality and avifauna use in a combined survey can provide appropriate information to conclude that the freshwater seepage points along the Inlet are important in maintaining landscape heterogeneity and attendant biodiversity.

In regard to saltmarsh vegetation, Cresswell & Bridgewater (1998) note that for many of the saltmarsh assemblages a large number of constituent ephemeral species tend to occur in winter-wet depressions in the marsh. This increases patch heterogeneity in the saltmarsh and thereby enhances the range and availability of the food resources. This would be a direct consequence of freshwater seepage effects. Cresswell & Bridgewater (1998) also discuss the occurrence of alien species in one of the more common saltmarsh assemblages of the Leschenault Inlet mudflats, and conclude that, generally, indirect human influence through environmental change is the main cause of the colonisation and proliferation of alien species in saltmarshes.

In many of the other major occurrences of similar saltmarsh systems in the estuarine systems in this region, there has been an increase in the abundance of alien species, probably due to the extensive disturbance suffered by these marshes from grazing and associated clearance. Associations in areas of dense human settlement tend to have greater numbers of alien species as constituents, with greater population numbers. The high quality of the saltmarshes of the Leschenault Inlet can be attributed to the remoteness from intensive human activity, which further enhances the quality of the marshes as a resource for the avifauna.

In relation to avifauna, the natural setting of the Leschenault Peninsula and Inlet provides important resources for many species of permanent and migratory waterfowl. The Peninsula itself provides protection from the strong westerly/south westerly winds, as well as providing a freshwater catchment and groundwater reservoir, which then seeps into the inlet well after the rains have ceased. This would be important for the many species of waterfowl having a daily requirement for fresh water whilst mainly feeding in the saline estuary. The length of the Peninsula is also important in that it provides a large area of differing habitats along its estuarine shore. Bird usage of the entire area, however, is extremely complex and would require much more intensive work to determine patterns in relationship to topography, feeding grounds, freshwater seepage, amongst others.

The shallow waters of the Inlet and associated mudflats during low tide provide feeding areas for avifauna, particularly given the extensive area and range of shallow water which provide a great variety of food sources. The shallowness of the Inlet also has restricted many forms of human recreation and commercial activity that would otherwise severely disturb waterfowl. Many species that are rarely seen in the region are present at different times of the year, such as the yellow-billed spoonbill (*Platalea flavipes*), a recent colonist to south-western Australia.

Importantly, the remoteness from human settlement and activity provides eremitic species with habitats that exist in few other places along this coastal sector due to increasing human settlement. The lack of major human disturbance to the environment of the Peninsula has been fundamental in maintaining the high ecosystem quality of the area.

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Peripheral wetland habitats and vegetation of the Leschenault Inlet estuary

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Abstract

Along the Leschenault Inlet estuary shore, interactions between ancestral landforms comprising the eastern shores, dune dynamics and the young western barrier dune shore, hydrodynamic processes, estuarine coastal processes, estuarine sedimentation, and a variable Holocene sealevel history, have resulted in a varied peripheral shore and wetland types. The shoreline habitats include supratidal tidal flats (vegetated dominantly by samphire), high tidal platforms (vegetated dominantly by samphire or rushes), tidal embayments (residing between dune corridors), high tidal platforms and dune interfaces, in zones of freshwater seepage (vegetated dominantly by rushes), cliffed sandy shores where coastal erosion is incising into dunes, steep dune shores where dunes are encroaching into the estuary, beachridges, spits, bar-and-lagoon complexes, stranded (relict) sand platforms, the Collie style deltaic complex, and the Preston style deltaic complex. Five broad categories of vegetation fringe the Leschenault Inlet estuary, classified on structure, salinity of habitat, and location relative to shore: 1) saltmarsh; 2) estuarine fringing forest; 3) fringing vegetation; 4) sandy rise vegetation; and 5) freshwater vegetation (forest and disturbance-related assemblages). Saltmarshes, comprising samphire and rush formations, develop in saline tidal areas. Estuarine fringing forest, typically small saltwater sheoak (*Casuarina obesa*), saltwater paperbark (*Melaleuca cuticularis*), paperbark (*Melaleuca viminea*), and swamp paperbark (*Melaleuca rhaphiophylla*), occurs as elevation increases and where soilwater salinity is not extreme. Fringing vegetation consists of emergent species living more or less permanently in shallow water (*e.g. Schoenoplectus validus*). Sandy rise vegetation occurs on the crest of barrier sand bars, on margins of high coastal sand dunes, or on low estuarine beach dunes. Freshwater fringing vegetation is close to the estuary in areas receiving substantial freshwater input.

There have been some marked changes in the peripheral vegetation of the estuary since 1941, some occurring in the vegetation alone, and some induced by estuarine coastal landform dynamics. These changes are evident as: 1) clearing of fringing vegetation; 2) decline of estuarine fringing forest; 3) encroachment of *Juncus kraussii* into the estuary; 4) colonisation of river deltas; and 5) formation of tidal lagoons or pools along the high tidal platforms.

There are four determinants at the large scale influencing the type and composition of saltmarsh present along the shore. The two most important are geomorphic setting and physical estuarine coastal processes. The third is a south to north gradient in source water salinity and the fourth is anthropogenic effects. Leschenault Inlet thus presents a heterogeneous array of shore habitats, resulting from a variable upland geomorphic setting (*i.e.* the south to north gradient along the west coast, and east coast *vs* west coast *vs* north coast setting), the variable coastal processes operating on the coast (to generate progradational mud flats *vs* cliffed dune shores *vs* bar-and-lagoon complexes *vs* tidal platforms), upland to estuarine groundwater hydrodynamics and interactions, deltaic build-up at river mouths, and a complex sealevel history to develop stranded estuarine landforms. In the Leschenault Inlet the complex array of estuarine coastal habitats, and the salinity gradients developed therein have resulted in a range of vegetation units that are distributed in mosaics and gradients across the various habitat types of the shoreline. In this context, Leschenault Inlet estuary represents a classic classroom for student studies and research into estuarine peripheral vegetation ecology. From this perspective, the shoreline habitats and vegetation comprising the periphery of the Leschenault Inlet estuary rank as most significant along the south-western coast of the Swan Coastal Plain, and ranks with the Walpole-Nornalup Inlet system which itself is located in the richest botanical district in south-western Australia.

Keywords: peripheral vegetation, saltmarsh, Leshenault Inlet, estuary, south-western Australia.

Introduction

For a small, relatively simple and young (wholly Holocene) estuary, Leschenault Inlet has generated a range of environmentally distinct habitats. This paper describes the development of geomorphic units (shore types) and habitat types fringing the estuary, and the various peripheral vegetation formations therein. As such, the objectives are to: 1) provide a geohistorical framework *i.e.* the sedimentologic and geomorphic evolution of the periphery of the estuary, in order to understand the development and distribution of the peripheral geomorphic units throughout Leschenault Inlet that provide vegetation habitats; 2) describe the relationship of habitat to vegetation complexes; 3) provide an inventory of the vegetation, and

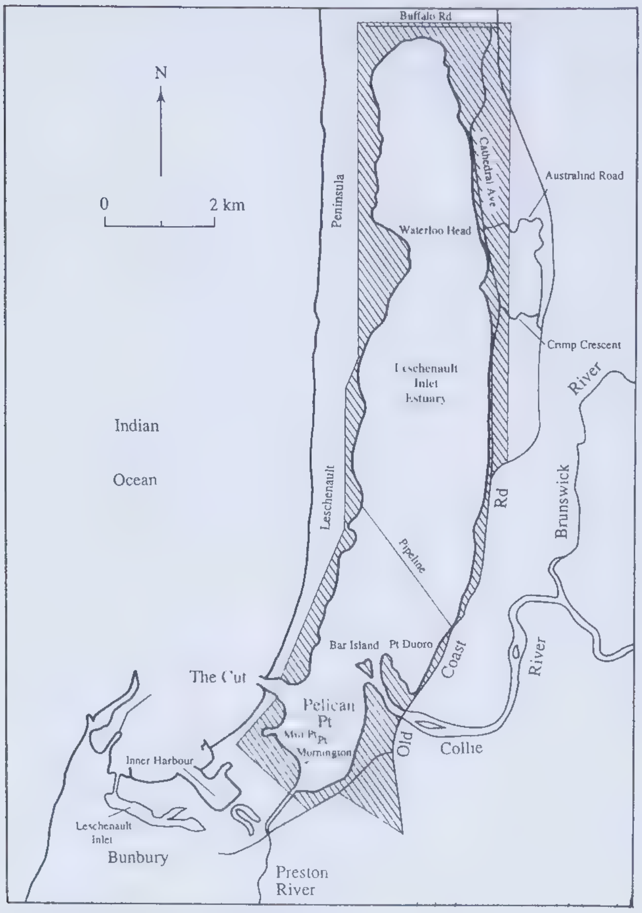


Figure 1. Location of study area.

a baseline of the vegetation associations fringing the estuary in terms of structure, composition and distribution; and 4) document the natural and anthropogenically induced changes to the peripheral vegetation of the area over the past 50 years.

Methods and terminology

Colour aerial photographs at 1:10 000 scale from the Department of Land Administration (WA) were obtained for the study area in 1989 from which sketch maps showing distribution of vegetation and vegetation type, standing water and land use (*e.g.* pasture or urban) were produced using a Zeiss Aerosketchmaster to a 1:5 000 scale. The maps were ground-truthed in the field on the 24th May, and the 8th and 21st June 1991, and annotated with relevant information on plant assemblage composition and structure and weed infestation. Plant assemblages were identified and described on the bases of structure and dominant species, after Trudgeon (1984), to provide a continuity of the description of the vegetation in this region. Unknown plant species were submitted to the WA Herbarium for identification.

Changes in the estuarine shoreline and the evolution of small scale geomorphic features, and habitats, and changes in vegetation were noted by comparing the field observations and mapping in 1991 with those evident on aerial photographs from 1941, 1966, 1975, 1977, 1982, 1986 and 1989. Examples of such changes were assessed by reducing maps of the distribution of the plant assemblages at particular places and times to the same scale using the Zeiss Aerosketchmaster.

Transects through selected habitats and vegetation units were established to describe the habitat types and vegetation. These transects were surveyed with respect to Australian Height Datum, and sites along the transect were established to describe sediments, stratigraphy, and groundwater. Data from these transects in terms of profiles, stratigraphy, and groundwater are presented in Semeniuk (2000) and Semeniuk *et al.* (2000). The extent of the study area, and the geographic locations mentioned in the text are shown in Fig 1.

The terms "peripheral habitats" and "peripheral vegetation" in this paper refer to the wholly high-tidal to supratidal habitats and vegetation, respectively, that fringe the periphery of the Leschenault Inlet estuarine lagoon. All habitats along the estuary periphery that originate from estuarine processes are incorporated in this term (*e.g.* high-tidal flats, spits, stranded platforms), including those stranded estuarine-derived landforms developed when sealevel was higher than at present. The term "saltmarsh" refers to grass, rush, sedge, and/or samphire vegetation formations that are regularly inundated and inhabit the saline to brackish environments fringing the estuary. The term "samphire" is used to denote chenopod low herbland formations. The term "mangrove" refers to tree and shrub vegetation formations that are regularly inundated and inhabit the saline to brackish environments fringing the estuary. For the tidal heights, MSL refers to mean sea level, AHD is the Australian Height Datum, and HAT refers to the highest astronomical tide.

Regional setting

Leschenault Inlet is a shallow estuarine lagoon located along the south-western coast of the Swan Coastal Plain (Semeniuk & Meagher 1981), and separated from the Indian Ocean and Rottnest Shelf by barrier dunes (Semeniuk & Searle 1985). The estuarine lagoon is located in a subtropical subhumid climate, or Mediterranean climate (Gentilli 1972), with an annual rainfall of *ca* 880 mm and annual evaporation of *ca* 1 980 mm. Tides are microtidal, with a prevailing range of 0.5 m and a maximum range of 0.9 m.

There are four main landform and estuarine units that constitute the Leschenault Inlet system; these are (Fig 2) : 1) an eastern hinterland: a high ridge of quartz sand and limestone (the Mandurah-Eaton Ridge), and lowlands underlain by limestone (the southern extremity of the Yalgorup Plain; Semeniuk 1995, 1997); 2) Leschenault Inlet itself: an elongate shore parallel, estuarine lagoon; 3) the western barrier dunes (Leschenault Peninsula): a quartz/carbonate sand barrier that bars Leschenault Inlet (Semeniuk & Meagher 1981); and 4) delta-lands, formed by the Collie River and Preston River that enter the estuarine lagoon to its south-east and south. Leschenault Inlet estuary, however, is not in a pristine condition. The nature of the internal geomorphology of the majority of the Leschenault Inlet estuarine lagoon, however, has remained unchanged.

In terms of its natural internal geomorphology, the Leschenault Inlet area has been subdivided into a number of estuarine and deltaic geomorphic units (modified from Wurm & Semeniuk 2000, and Semeniuk 2000): 1) central and northern subtidal basins; 2) eastern and western subtidal platforms and ramps; 3) high-tidal platforms; 4) northern supratidal flat; 5) beachridges, spits, and bar-and-lagoon complexes; 6) the Collie River delta; and 7) the Preston River delta.

The central and northern basins and the aquatic eastern and western platforms and ramps, within the estuary, being subtidal or low intertidal, are not inhabited by peripheral estuarine vegetation, and are outside the scope of this paper. In the high intertidal zone, both east and west shores of the estuarine lagoon are composed mainly of herbaceous vegetated high tidal platforms (saltmarsh). The northern Leschenault Inlet is bordered by a broad supratidal flat; this surface is nearly horizontal, to very gently inclined towards the estuary, emergent by progradation, underlain by mud, and vegetated by samphire. Along the margin of the western shore, there are locally developed beachridges, spits, and bar-and-lagoon complexes. Spits emanate from eroding dune tips, projecting onto the tidal zone of the estuary, generally traversing an interdune corridor or embayment. Where spits have encroached fully across an interdune corridor or embayment, the embayment may be barred, forming a bar-and-lagoon system.

In the south-eastern part of Leschenault Inlet, the Collie River has built a triangular wave-dominated delta of distributary channels, beachridges and samphire-vegetated swales and lagoons. The remnant of the Preston River delta, in the southern extremity of the former more longitudinally extensive estuarine lagoon, is composed of linear tidal-current-aligned shoals and emergent islands, with intervening shallow channels. Emergent islands within the Preston River delta are vegetated by samphires, rushes, or mangrove in the tidal zone, and terrestrial vegetation in the supratidal zone.

Wurm & Semeniuk (2000) subdivide the estuary into four salinity fields, based mainly on the seasonal variability of the estuarine waters (Fig 2). These salinity fields are important to understanding the distribution of species comprising the peripheral vegetation in that the various water bodies therein provide the source water for recharge to the tidal flats. They are: 1) an upper estuary field where mean salinities approximate marine water, but show large variation (brackish water common in winter, and hypersaline water common in summer); 2) a middle estuary field where mean salinities approximate marine water, but with some variation; 3) a lower estuary field close to the marine source where salinities are mostly marine, with little variation; and 4) a deltaic field where salinities mostly are marine, but with marked freshwater periods during river flooding.

Across the tidal flats, there is a gradient of increasing groundwater salinity, from marine at the estuary to hypersaline towards the land. The upslope hypersalinity is diluted by freshwater seepage at the boundary with upland dunes. The three main hydrologic sources and mechanisms that maintain the peripheral vegetation are:

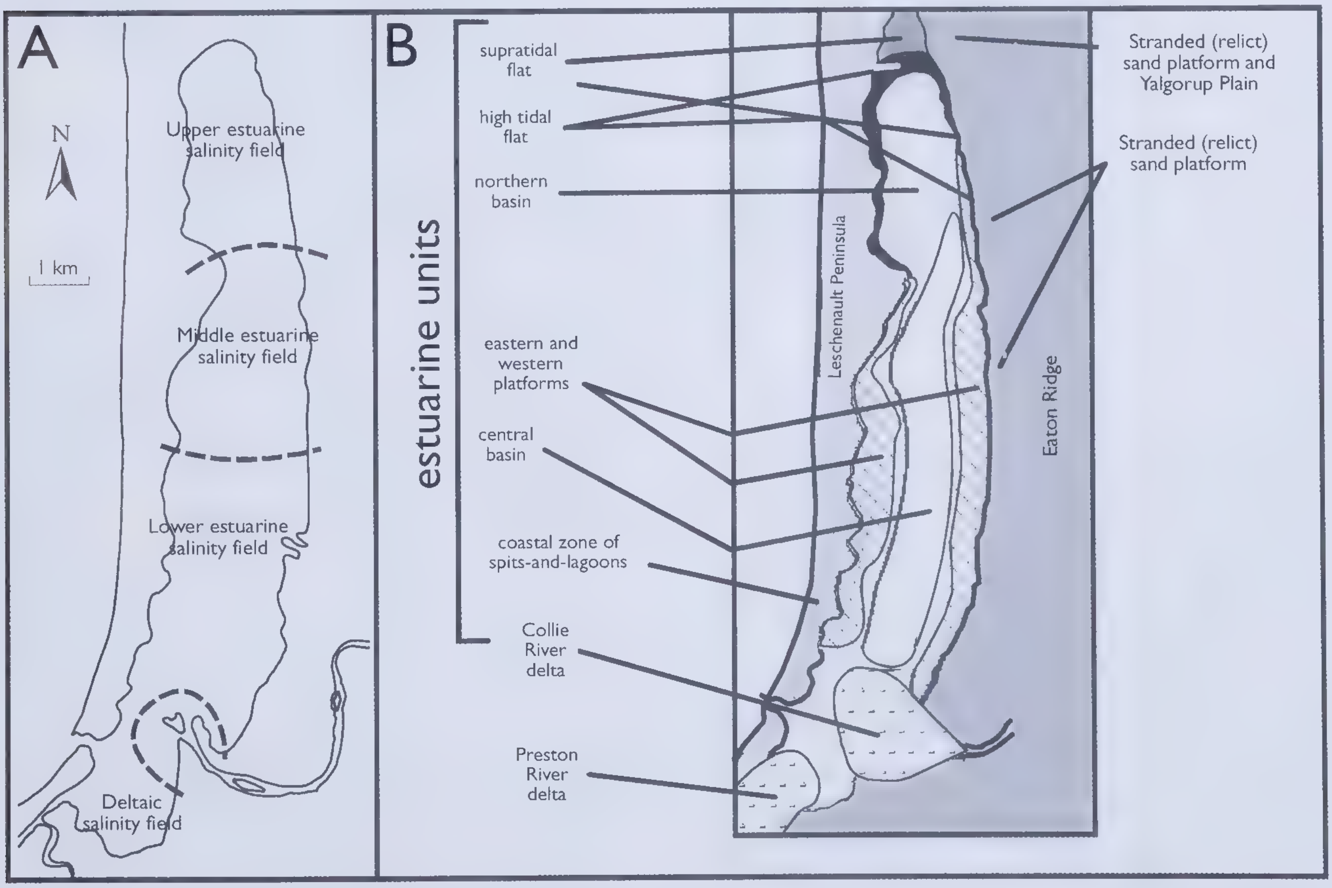

A
N
Upper estuarine salinity field
1 km
Middle estuarine salinity field
Lower estuarine salinity field
Deltaic salinity field
B
estuarine units
supratidal flat
high tidal flat
northern basin
eastern and western platforms
central basin
coastal zone of spits-and-lagoons
Collie River delta
Preston River delta
Leschenault Peninsula
Eaton Ridge
Stranded (relict) sand platform and Yalgorup Plain
Stranded (relict) sand platform

Figure 2. A: The estuarine salinity framework in Leschenault Inlet (after Wurm & Semeniuk 2000). **B:** The main landform and estuarine units comprising the Leschenault Inlet system (an eastern hinterland; Leschenault Inlet itself; the western barrier dunes; delta-lands).

1) tidal recharge that replenishes saline water to the high tidal flats; 2) meteoric recharge that directly reduces the salinity of these tidal flats; and 3) freshwater seepage from the dunes that reduces hypersalinity along the interface between the tidal flat and dune shore (Cresswell 2000).

Evolution of geomorphic units and shore types

Viewed at the largest scale, the sedimentary and geomorphic patterns of the Leschenault Inlet area are relatively simple. A shore-parallel linear barrier dune complex bars an estuarine lagoon from the open Indian Ocean. The barrier dune complex has been retreating eastwards over the estuarine sediment throughout the Holocene through a staggered series of parabolic dune incursions that spill over into the estuary (Semeniuk 1985). The sheltered interior of the estuarine lagoon is accumulating mud, muddy sand, and locally sand, and shelly equivalents of these sediments (Semeniuk 2000). To the east, these estuarine sediments onlap a hinterland of Pleistocene sediments, or onlap or interfinger with sediments derived from this Pleistocene basement.

At the smaller scale, mobile parabolic dunes directly spill into the estuary, forming sandy aprons in the aquatic environment. Laterally, muddy estuarine sediments accumulate, later to be buried by an encroaching dune. The staggered dune encroachment into the estuary, with dune sand fingers laterally alternating with muddy accumulations in sheltered corridors develop variable inter-digitating and complex interfaces between dune sand and estuarine sediment.

The main physical processes operating in Leschenault Inlet that transport, shape, and develop sediment bodies in both the estuarine environment and the peripheral geomorphic units, are: 1) wind-induced wave action on shores and platforms; 2) wind-induced currents; 3) storm waves; 4) tidal flooding; 5) tidal current erosion and transport; 6) tidal current deposition; 7) riverine flooding; and 8) wind erosion and transport. The effects of these processes in shaping the sedimentary environments are described below in terms of the process and its main location, and its main effects.

Wind-induced wave action on shores and east and west platforms reworks sand on the eastern platform, generally removing mud. It also reworks sediment on the western platform partly removing mud, and erodes the sandy shores and the small mud cliff shores. Wind-induced currents on the east and west shores transport mud reworked by wave action into suspension to the northern basin and supratidal environments and transport sand, shaping the spits and bars. Storm waves on east and west shores, the north-facing sector of Collie River delta, and the northern supratidal flat build low storm beachridges, transport shells onto the high tide and supratidal zone, winnow sediment along the shore, and erode the small cliff shores. Tidal flooding within the Preston River delta and the artificial tidal delta shapes and deposits sediment on the tidal delta and Preston River delta. Tidal current erosion and transport along the east and west shores also erodes and transports sand along the shore to build spits and bars. Tidal current deposition on the high-tidal platform and the northern mud basin and supratidal flat accumulates mud onto the high-tidal environments. Riverine flooding at the mouth of the Collie River delta injects riverine sand and mud into the estuary. Wind erosion/transport on the east- and west-located sandy beaches develops small beachridges and dunes that fringe the estuary shore, and builds the spits and bars.

The general accretionary sedimentary history of Leschenault Inlet has been complicated by a variable sealevel history, which has resulted in the stranding of some geomorphic units, or in the placing of some estuarine-derived units close to the water table (hence they have become estuarine peripheral wetlands). The history of sealevel is described by Semeniuk (1985) in three stages: 1) sealevel stage 1: 7 000-4 500 years BP, with sealevel 2-3 m below present level; 2) sealevel stage 2: 4 500-*ca* 3 500 years BP, with sealevel 3-4 m above present; and 3) sealevel stage 3: 2 800 years BP to present, with sealevel at present height.

Peripheral geomorphic units or wetlands developed during sealevel stage 1 have not been preserved. The effect of the sealevel stage 2 highstand is evident on the eastern shore: the eastern platform extant during the 3-4 m sealevel highstand is preserved now as an elevated platform underlain by structureless quartz sand, whose surface is 1-2 m above present sealevel (this surface would have been 1-1.5 m *below* sealevel during the highstand). However, most of the peripheral geomorphic units, habitats, and wetlands are related to present sealevel (sealevel stage 3).

With sealevel at its present position, sedimentation mainly involves: 1) development of the eastern platform as a wave-built structure at a level related to the current sealevel; 2) development of the western platform/ramp as parabolic dunes encroach into the estuary; 3) development of spits, evolving to bars and associated lagoons along the crenulate western shoreline; 4) development of high-tidal platforms through tidal mud accretion; 5) winnowing of mud from subaquatic platforms and the central basin, and its transport northwards into the northern basin; 6) shoaling of the northern basin to develop the northern supratidal flat; 7) injection of fluvial sand and mud into the estuary to develop deltas; and 8) tidal reworking of the Preston River delta to develop tidal-dominated estuarine landforms.

Shoreline habitats

The following shore types, and their vegetation, either developed earlier in the Holocene (Stage 2 sealevel history), or formed with sealevel at its present position (Stage 3 sealevel history), are recognised along the periphery of the Leschenault Inlet estuary: 1) supratidal tidal flats (vegetated dominantly by samphire); 2) high tidal platforms (vegetated dominantly by samphire or rushes); 3) tidal embayments (residing between dune corridors); 4) high tidal platforms and dune interfaces, in zones of freshwater seepage (vegetated dominantly by rushes); 5) cliffed sandy shores where coastal erosion is incising into dunes; 6) steep dune shores where dunes are encroaching into the estuary; 7) beachridges; 8) spits; 9) bar-and-lagoon complexes; 10) stranded (relict) sand platforms; 11) the Collie style deltaic complex; and 12) the Preston style deltaic complex. A brief description of these units is given below and a selection of the larger units are shown in Fig 3.

The supratidal tidal flats are broad and extensive, low

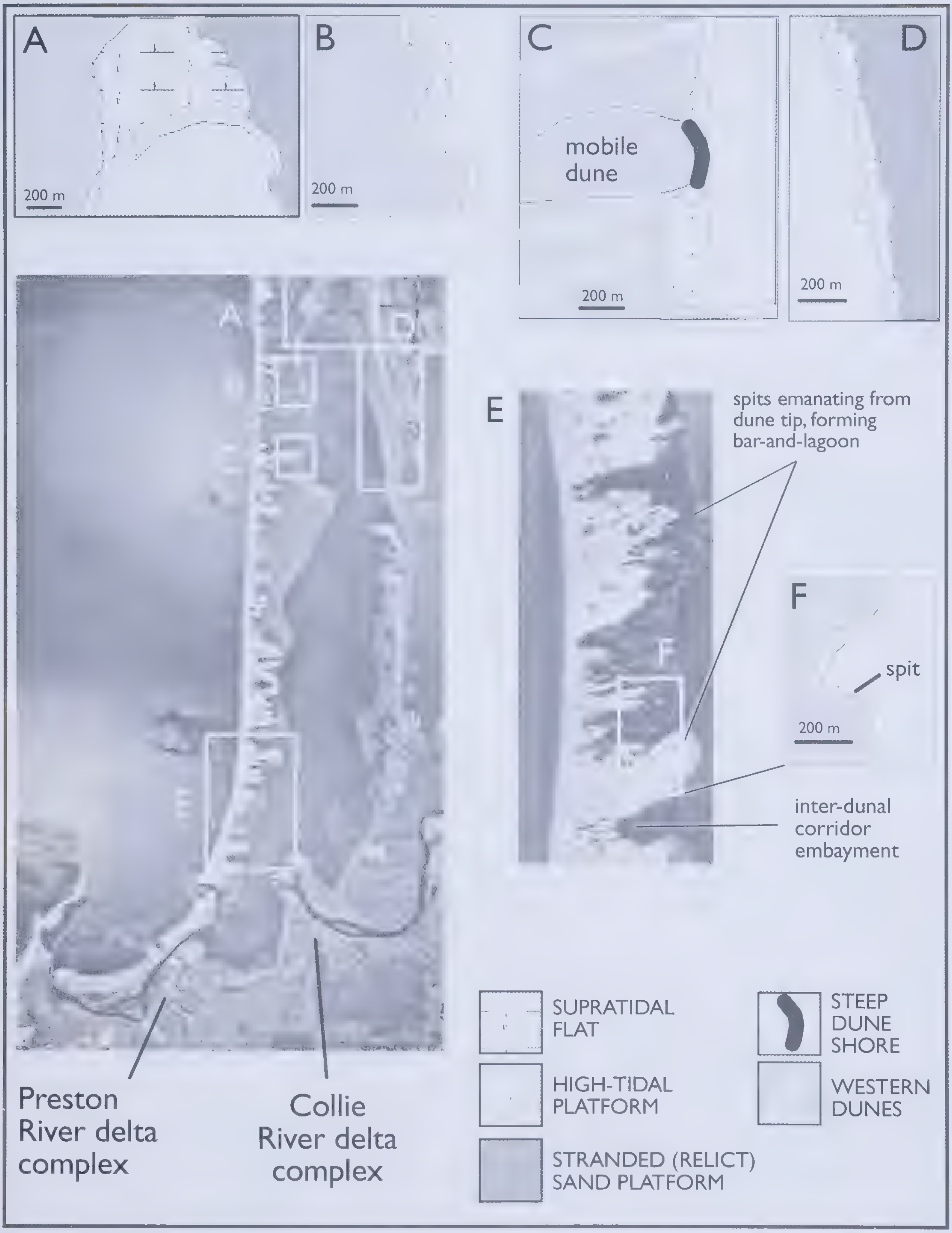

A
200 m
B
200 m
C
mobile dune
200 m
D
200 m
A
B
C
D
E
E
spits emanating from dune tip, forming bar-and-lagoon
F
F
spit
200 m
inter-dunal corridor embayment
Preston River delta complex
Collie River delta complex
SUPRATIDAL FLAT
HIGH-TIDAL PLATFORM
STRANDED (RELICT) SAND PLATFORM
STEEP DUNE SHORE
WESTERN DUNES

Figure 3. Typical location and detail of the various habitat units: supratidal tidal flats (vegetated dominantly by samphire); high tidal platforms (vegetated dominantly by samphire or rushes); tidal embayments (residing between dune corridors); high tidal platforms and dune interfaces, in zones of freshwater seepage (vegetated dominantly by rushes); cliffed sandy shores where coastal erosion is incising into dunes; steep dune shores where dunes are encroaching into the estuary; beachridges; spits; bar-and-lagoon complexes; stranded (relict) sand platforms; the Collie style deltaic complex; the Preston style deltaic complex.

gradient flats, at and above HAT, underlain by mud, and vegetated by samphires, situated along the northern margin of the estuary. The high tidal platforms are broad and lengthy, low-gradient flats between MSL and HAT, vegetated by samphire or rushes, locally containing shore-parallel low relief mud bars, and intervening shallow shore-parallel lagoons, particularly in western and north-western locations, and commonly terminated at their estuary end by a small cliff (< 30 cm high). They are underlain by mud, located along the north-eastern margin and entire western margin of the Inlet. Narrow platforms also border the eastern margin of the estuary. The tidal embayments (residing between dune corridors) are broad, but areally restricted, low-gradient tidal flats grading to barred water bodies, at MSL to above HAT, underlain by mud, and located along south-western margins of the estuary. The high tidal platforms and dune interfaces are narrow, low gradient flats, situated at and above HAT, underlain by muddy sand and sand, and vegetated by rushes. They are located along the south-western and mid-western margins of the estuary. Cliffed sandy shores are narrow cliff zones located along south-western and mid-western margins of the estuary, and are formed where coastal erosion is incising old dunes. Steep dune shores are narrow, moderate gradient flats, situated at and above HAT, underlain by sand. They are located along the south-western and mid-western margins of the Inlet where dunes are encroaching into the estuary. Beachridges, low-relief, shore-parallel bars of sand formed at and above HAT, are located along western and eastern margins of the estuary. Spits are low relief shore-parallel bars of sand emanating from an eroding dune tip, traversing an embayment, formed at and above HAT. They are located along the western and eastern margins of the estuary. The bar-and-lagoon complexes are broad, but areally restricted, low gradient tidal flats and barred water bodies, at MSL to above HAT, underlain by mud, and barred by a sand body, and located along the south-western margin of the estuary. Stranded (relict) sand platforms are broad, low-gradient flats, underlain by sand with locally developed relict beachridges and sand waves. Their surfaces are situated up to 1 m above HAT. They are located along the eastern margin of the estuary. The Collie River deltaic complex overall is a triangular low-relief fluvially-dominated to wave-dominated deltaic landform projecting into the estuary at its south-eastern margin, composed of distributary channels, abandoned channels, levee banks, beachridges, swales, subaerial deltaic flats, subaqueous deltaic mouth bars and shoals, and delta front sand flats, shoals and sand waves. It is a fluvial dominated delta with a component of wave reworking developing the beachridge complexes on the northern sector. The Preston River deltaic complex overall is a triangular low-relief tide-dominated deltaic landform originally located along the southern part of the estuary, and comprised of distributary channels, oval to elliptical (emergent to submerged) shoals oriented parallel to the tidal flow, abandoned channels, and levee banks.

Overview of peripheral vegetation

The peripheral vegetation of the Leschenault Inlet estuary has been noted, mapped, or described as part of scientific studies, floral surveys, and unpublished reports by a number of authors, including Diels (1906), Sauer (1965), Smith (1985), Saenger *et al.* (1977), Schwinghammer (1982), Semeniuk *et al* (1978), Semeniuk & Meagher (1981), Trudgeon (1984), Bridgewater (1982, 1985, 1989), Pen (1992), Cresswell & Bridgewater (1998), and Bridgewater & Cresswell (1999). Also, Semeniuk *et al.* (1989) describes Quindalup vegetation pertinent to Leschenault Inlet. Biogeographically, the peripheral vegetation of the Leschenault Inlet estuarine lagoon belongs to Mediterranean Saltmarsh Biogeographic Zone of Bridgewater (1982), and the junction of the Mediterranean and Western transition zones of Bridgewater & Cresswell (1999). This indicates the key boundary position of the Leschenault Inlet in biogeographical terms, a point recognised for the hinterland region by Bridgewater (1994).

Cresswell & Bridgewater (1998) recognise a range of vegetation associations from south-western Australia, of which the following are found peripheral to the Leschenault Inlet estuary: 1) Avicennio-Sarcocornietum quinqueflorae P B Bridgewater 1982, with the identifying species *Avicennia marina* and *Sarcocornia quinqueflora;* 2)Sarcocornio-Suaedetum australis P B Bridgewater 1982, with the identifying species *Sarcocornia quinqueflora* and *Suaeda australis.* In the Leschenault area the sub-association, *halosarcietosum halocnemoidis* (with the diagnostic species *H. halocnemoides halocnemoides*); 3) Juncetum kraussii P B Bridgewater 1982, with the identifying species *Juncus kraussii* and *Samolus repens;* and 4) Halosarcietum halocnemoidis P B Bridgewater 1982, with the identifying species *Halosarcia halocnemoides* ssp *halocnemoides.*

Halosarcietum pergranulatae P B Bridgewater 1982, with the identifying species *Halosarcia pergranulata* ssp *pergranulata* is another association that has been noted in this region, and potentially could have occurred in the Leschenault Inlet area. However, Trudgeon (1984) did not record the identifying species, and Pen (1992) also did not find this association within his surveys. The association may be restricted to the Peel-Harvey estuary.

Peripheral shore types, habitats, and vegetation

Vegetation fringing Leschenault Inlet estuary can be divided into five types based on structure, salinity of habitat, and location relative to the shore : these are discussed below in terms of vegetation type, large-scale estuarine and salinity setting, smaller scale vegetation types. The saltmarsh is located on supratidal tidal flats, high tidal platforms, tidal embayments (residing between dune corridors), high tidal platforms and dune interfaces, and Collie River deltaic complex, saline to brackish high-tidal platforms, and swales and abandoned channels of the deltas. The saltmarsh formations consist of samphire flats and heath, and open to closed low sedgelands, rushlands, and herblands. The estuarine fringing forest is located on supratidal tidal flats, high tidal platforms, tidal embayments (residing between dune corridors), stranded (relict) sand platforms, the Preston River deltaic complex, and saline to freshwater tidal to supratidal settings. It consists of mangrove, or saltwater paperbark, or some freshwater paperbark. Fringing vegetation is located on supratidal tidal flats, and stranded (relict) sand platforms, and freshwater supratidal setting. It consists of emergent sedge, and sedge and mat grass formations. Sandy rise vegetation occurs on cliffed sandy shores, steep dune shores, beachridges, spits, part of bar-and-lagoon complexes, on the Collie River and Preston River deltaic complexes, as well as freshwater dune margins, spits, bars, and beaches. It consists of open shrubland, woodland, closed sedgeland, low closed Acacia scrub and thicket. Freshwater vegetation (forests) occurs on stranded (relict) sand platforms, and the mostly freshwater setting of the eastern shore stranded platform. It consists of sedgeland, and low open - closed forest. Freshwater vegetation (that is disturbance-related) is located on stranded (relict) sand platforms, and the mostly freshwater setting of the eastern shore stranded platform. It consists of remnant forest and woodlands with weed or pasture dominant in understorey, and weed assemblages.

Saltmarshes, comprising samphire and rush formations, develop in saline tidal areas. Estuarine fringing forest, typically of the small saltwater sheoak (*Casuarina obesa*), saltwater paperbark (*Melaleuca cuticularis*), paperbark (*Melaleuca viminea*), and swamp paperbark (*Melaleuca rhaphiophylla*), occurs as the elevation increases and where soilwater salinity is not extreme. Fringing vegetation consists of those emergent species which live more or less permanently in shallow water (*e.g. Schoenoplectus validus*). Sandy rise vegetation occurs on the crest of barrier sand bars, on margins of high coastal sand dunes, or on low estuarine beach dunes. Freshwater fringing vegetation occurs close to the estuary in areas receiving substantial freshwater input, either from surface inputs (*i.e.* drains, creeks) or from groundwater seepage which typically occurs at the base of a ridge or sand dune.

In areas subject to frequent disturbance, plant assemblages may develop which are marked by an absence of native plant regeneration and/or exhibit a high degree of weed infestation and heterogeneity. For example, relic native trees forming parkland over pasture are largely prevented from regenerating because of continuous disturbance such as grazing and fires, and the population becomes increasingly aged. Disturbance-related plant assemblages also develop where environmental conditions have not reached an equilibrium with changing land use over a period of many years. In such cases some native plant species undergo decline, others become established, while others maintain their populations, and at the same time ephemeral weeds establish opportunistically. Such assemblages appear chaotic and contrast greatly with the homogeneity of relatively stable native plant assemblages.

The vegetation types within the various shore types and peripheral habitats are briefly described in Table 1 below. The main species composition of the vegetation types are described later in the text.

From a large scale perspective, the peripheral vegetation occurs in eleven main geographic areas : 1) northern supratidal flats; 2) western high-tidal platforms; 3) south-western high-tidal platforms; 4) south-western shore of spits and bar-and-lagoons; 5) north-eastern high-tidal platforms; 6) eastern high-tidal platforms; 7) eastern stranded platform; 8) barrier/tidal platform edge; 9) steep dune shores; 10) Collie River delta; and 11) Preston River delta. The distribution of the vegetation types around the estuary is presented as a series of maps. Fig 4 shows the location

Table 1. Relation between habitat type and vegetation

Habitat unit	Vegetation types
supratidal tidal flats	vegetated dominantly by saltmarsh (samphire)
high tidal platforms	vegetated dominantly by saltmarsh (samphire, followed to landward by rushes)
tidal embayments	vegetated by saltmarsh (samphires and rushes)
high tidal platforms and dune interfaces, in zones of freshwater seepage	vegetated dominantly by saltmarsh (samphires and rushes), backed by fringing forest
cliffed sandy shores	no peripheral estuarine vegetation
steep dune shores	mangroves, or rushes
beachridges	sandy rise vegetation (see text)
spits	sandy rise vegetation (see text)
bar-and-lagoon complexes	sandy rise vegetation (see text), and freshwater vegetation
stranded (relict) sand platforms	*Juncus kraussii* rush, followed to landward by low forests of *Melaleuca cuticularis* and occasionally *Casuarina obesa*, or by *Melaleuca rhaphiophylla* low forests
Collie River deltaic complex	mixed assemblages as mosaics according to intra-delta habitats: samphire in the sediment-filled abandoned channels, rushes lining the channels, and dune vegetation on spits and sand ridges
Preston River deltaic complex	mixed assemblages as mosaics according to intra-delta habitats: samphires and scattered mangrove colonising shoal crests, rush along channel margins and the interface between the barrier-dune and delta, mangroves bordering the emergent delta shoals, dune vegetation or Casuarina bordering emergent delta shoals

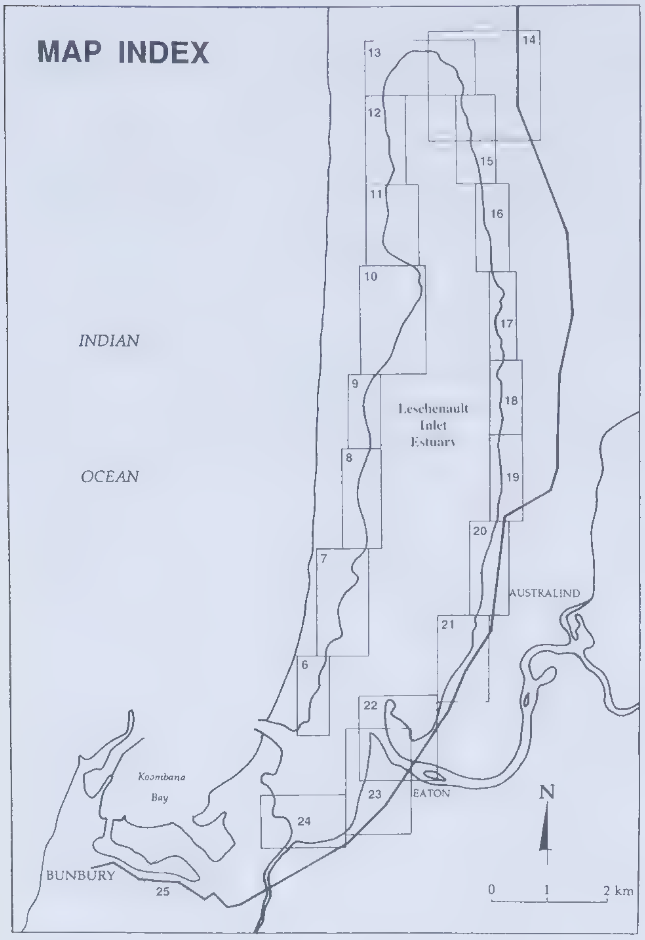


Figure 4. Location of detailed maps.

of detailed maps. Fig 5 shows the key to the vegetation units of the maps. Figs 6-25 show details of vegetation mapping along the estuarine shore. These maps provide a baseline of the distribution of vegetation types along the shore of the estuary in 1989.

Saltmarsh vegetation

***Juncus kraussii* closed rushland**. Much of the southern half of the estuary is ringed at the water's edge with a dense band of sea rush *J. kraussii*, 0.5 - 1.0 m high, up to 1.5 m high. The halophytes, *Sarcocornia quinqueflora* and *Suaeda australis*, are often found amongst it and sometimes the small saltwater sheoak *Casuarina obesa*, saltwater paperbark *Melaleuca cuticularis* and the shrub sea heath *Frankenia pauciflora* are found scattered across it. *Juncus kraussii* closed rushland also fringes the saltmarshes on their landward side, particularly along the western foreshore. On the landward side, bands of *J. kraussii* are often fringed with knotted club-rush *Isolepis nodosa* or twig-rush *Baumea juncea* and the herb marsh saltbush *Atriplex prostrata*. Along the water's edge along the lower southern foreshore, fringing bands of water couch *Paspalum vaginatum* are common. Along the eastern foreshore, particularly along its middle region, the *J. kraussii* closed rushland is being invaded by the alien grasses *Cynodon dactylon* (couch) and *Pennisetum clandestinum* (kikuyu) and *Carpobrotus edulis* (pigface).

***Sarcocornia quinqueflora* saltmarsh complex** (*e.g.* Figs 6, 9-19). This saltmarsh complex contains five assemblages which often are impractical to separate for mapping exercises in the field as they merge over broad areas. The characteristic common to all four assemblages is the pres-

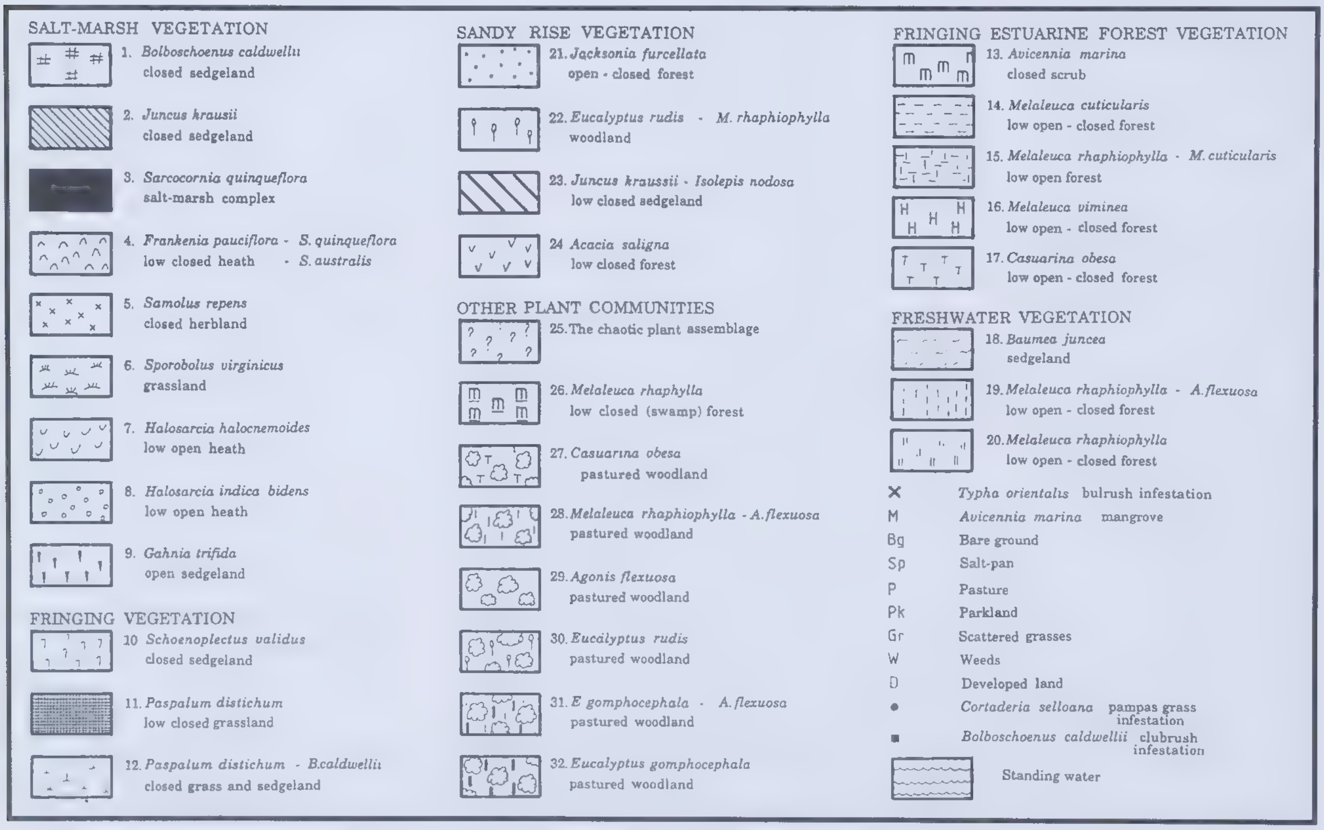
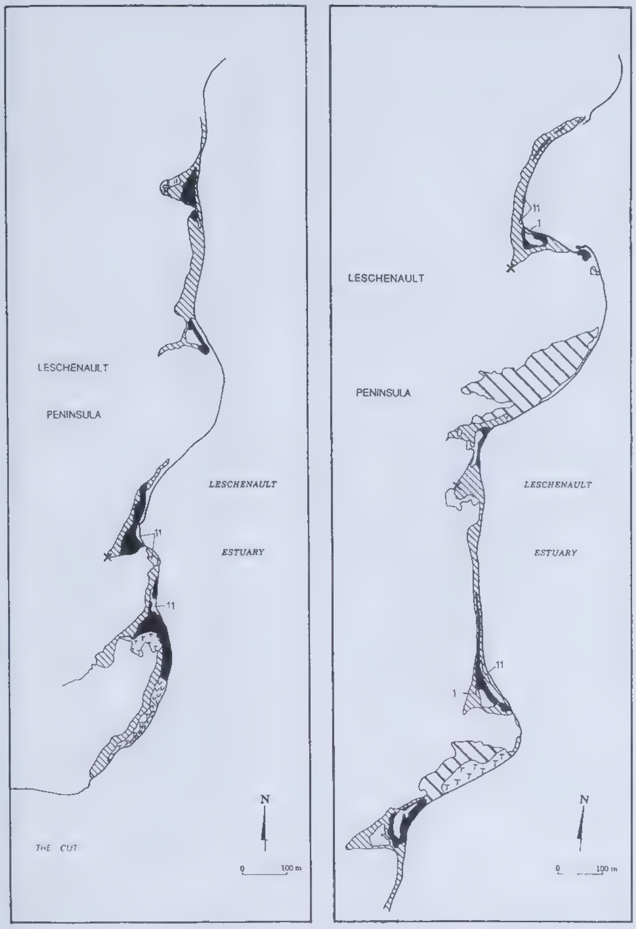
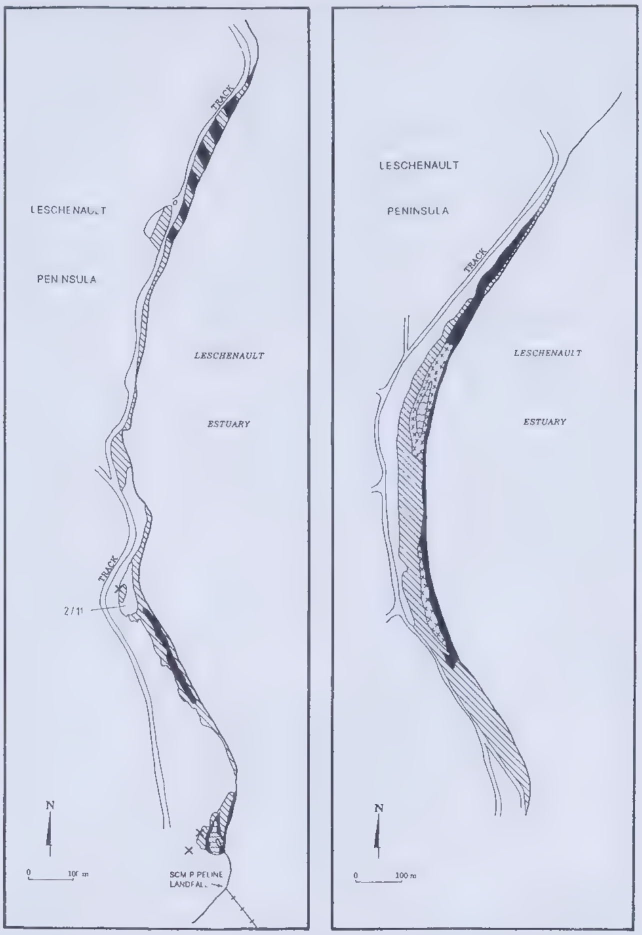

SALT-MARSH VEGETATION
1. Bolboschoenus caldwellii closed sedgeland
2. Juncus krausii closed sedgeland
3. Sarcocornia quinqueflora salt-marsh complex
4. Frankenia pauciflora - S. quinqueflora - S. australis low closed heath
5. Samolus repens closed herbland
6. Sporobolus virginicus grassland
7. Halosarcia halocnemoides low open heath
8. Halosarcia indica bidens low open heath
9. Gahnia trifida open sedgeland
FRINGING VEGETATION
10 Schoenoplectus validus closed sedgeland
11. Paspalum distichum low closed grassland
12. Paspalum distichum - B.caldwellii closed grass and sedgeland
SANDY RISE VEGETATION
21. Jacksonia furcellata open - closed forest
22. Eucalyptus rudis - M. rhaphiophylla woodland
23. Juncus kraussii - Isolepis nodosa low closed sedgeland
24 Acacia saligna low closed forest
OTHER PLANT COMMUNITIES
25. The chaotic plant assemblage
26. Melaleuca rhaphylla low closed (swamp) forest
27. Casuarina obesa pastured woodland
28. Melaleuca rhaphiophylla - A.flexuosa pastured woodland
29. Agonis flexuosa pastured woodland
30. Eucalyptus rudis pastured woodland
31. E gomphocephala - A. flexuosa pastured woodland
32. Eucalyptus gomphocephala pastured woodland
FRINGING ESTUARINE FOREST VEGETATION
13. Avicennia marina closed scrub
14. Melaleuca cuticularis low open - closed forest
15. Melaleuca rhaphiophylla - M. cuticularis low open forest
16. Melaleuca viminea low open - closed forest
17. Casuarina obesa low open - closed forest
FRESHWATER VEGETATION
18. Baumea juncea sedgeland
19. Melaleuca rhaphiophylla - A.flexuosa low open - closed forest
20. Melaleuca rhaphiophylla low open - closed forest
× Typha orientalis bulrush infestation
M Avicennia marina mangrove
Bg Bare ground
Sp Salt-pan
P Pasture
Pk Parkland
Gr Scattered grasses
W Weeds
D Developed land
● Cortaderia selloana pampas grass infestation
■ Bolboschoenus caldwellii clubrush infestation
Standing water

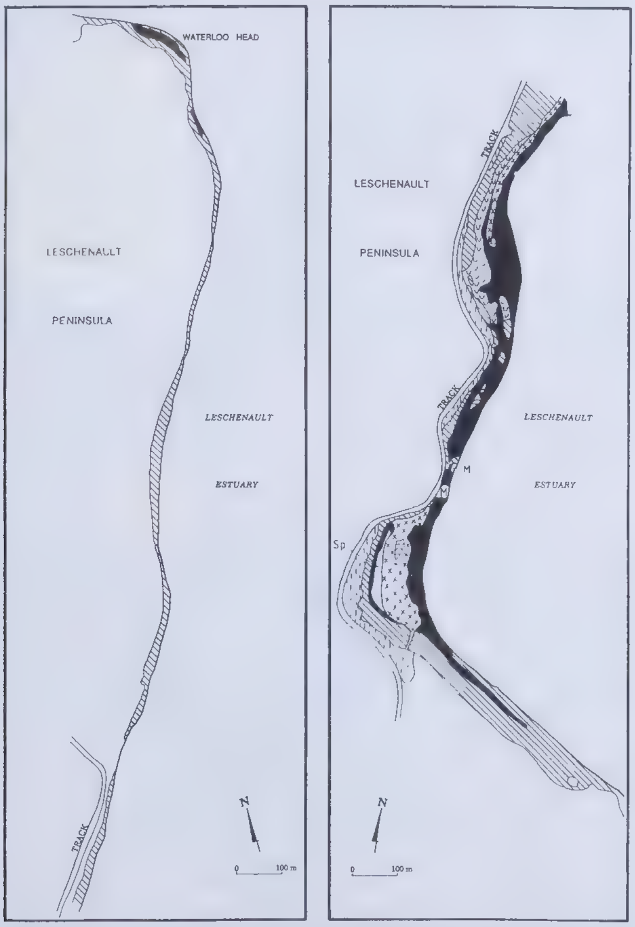
Figure 5. Key to vegetation units for maps presented in Figs 6-25.



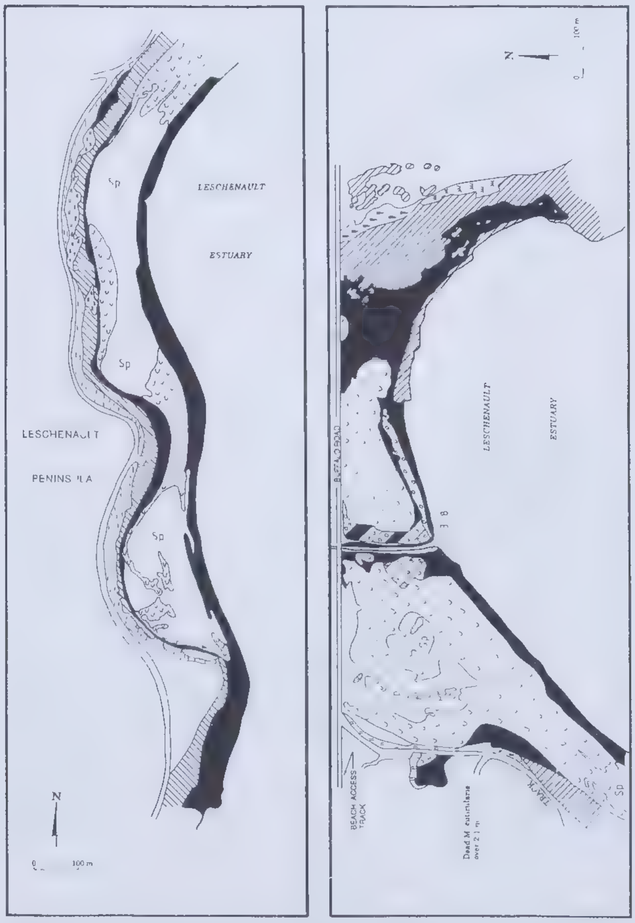
Figures 6-7. South-western estuarine shore showing vegetation units



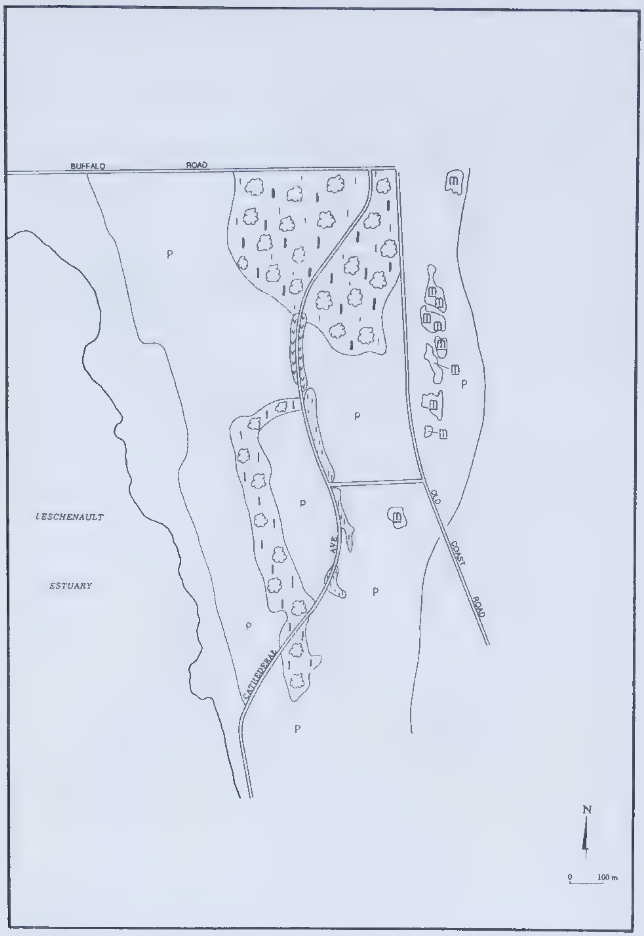
Figures 8-9. Western estuarine shore showing vegetation units.



Figures 10-11. Western estuarine shore showing vegetation units.



Figures 12-13. North-western estuarine shore showing vegetation units.



Figures 14. North-eastern estuarine shore showing vegetation units.

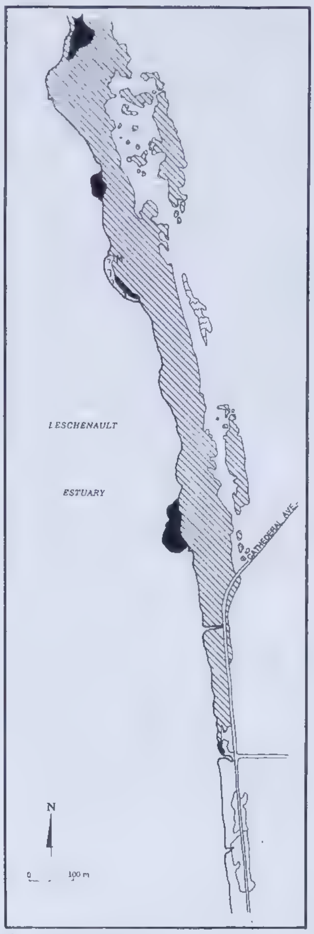


Figure 15. North-eastern estuarine shore showing vegetation units.

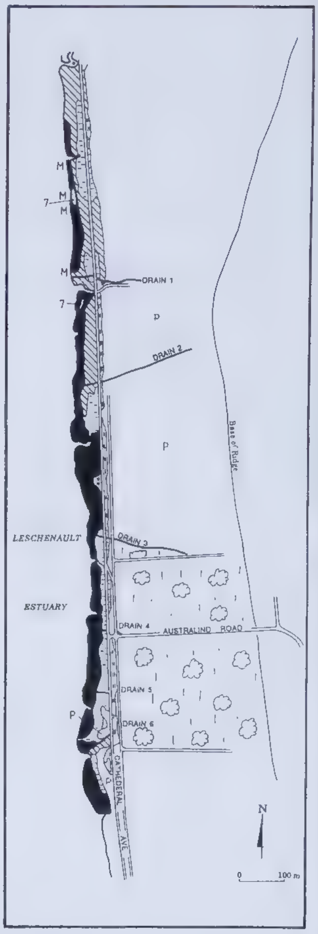
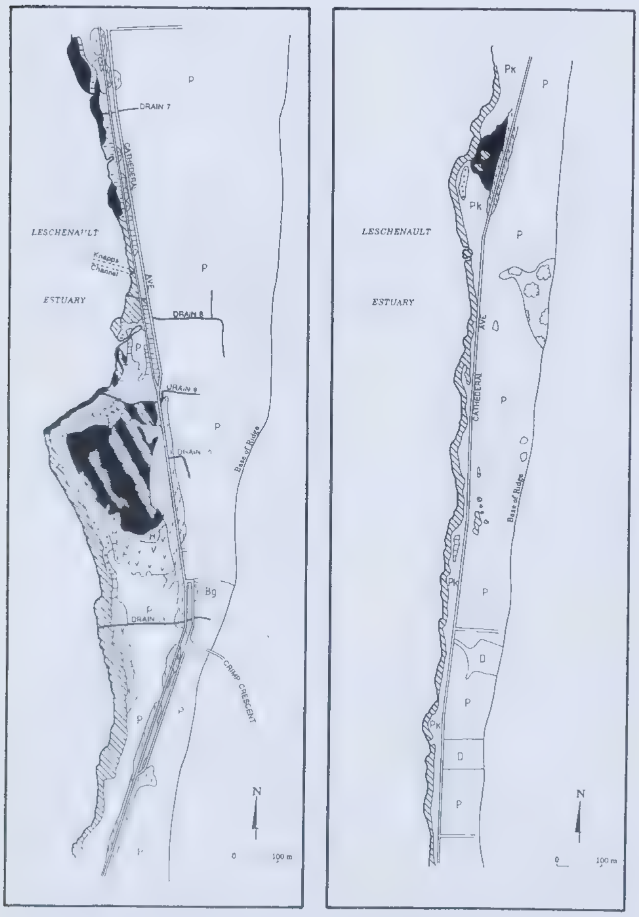
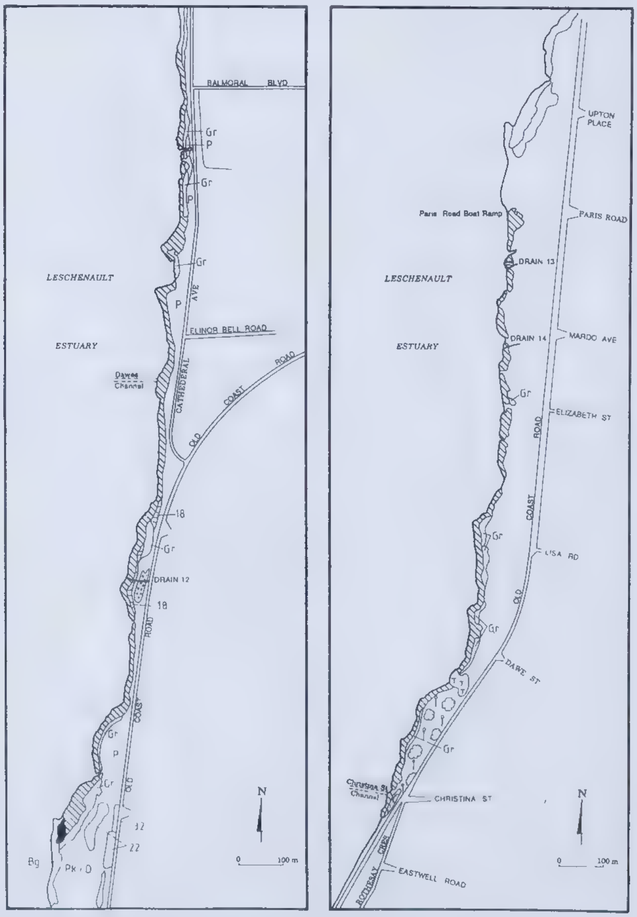


Figure 16. Eastern estuarine shore showing vegetation units.



Figures 17-18. Eastern estuarine shore showing vegetation units.



Figures 19-20. Eastern estuarine shore showing vegetation units.

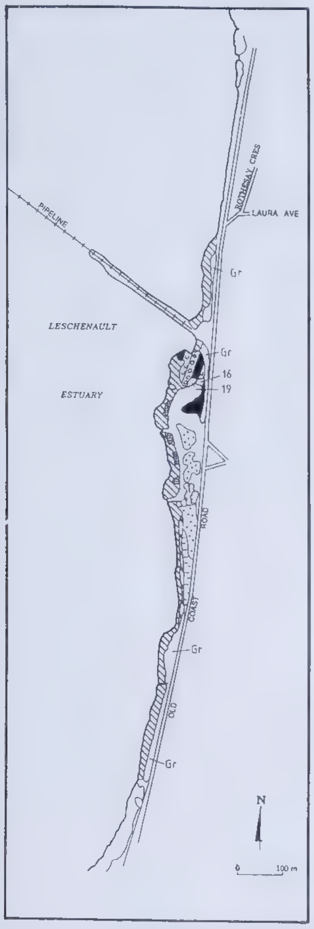


Figure 21. South-eastern estuarine shore showing vegetation units.

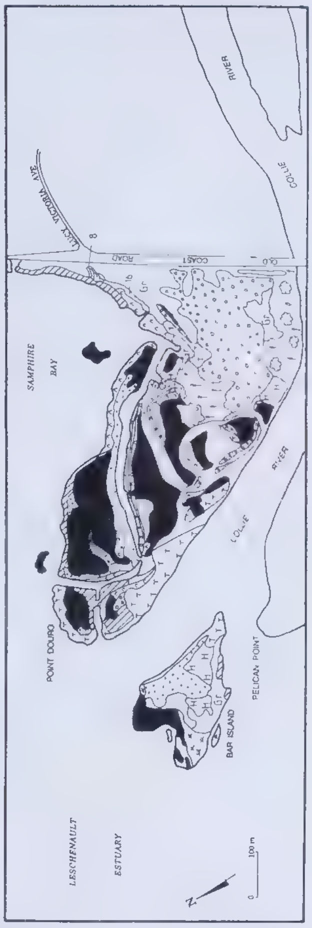


Figure 22. Collie River delta showing vegetation units.

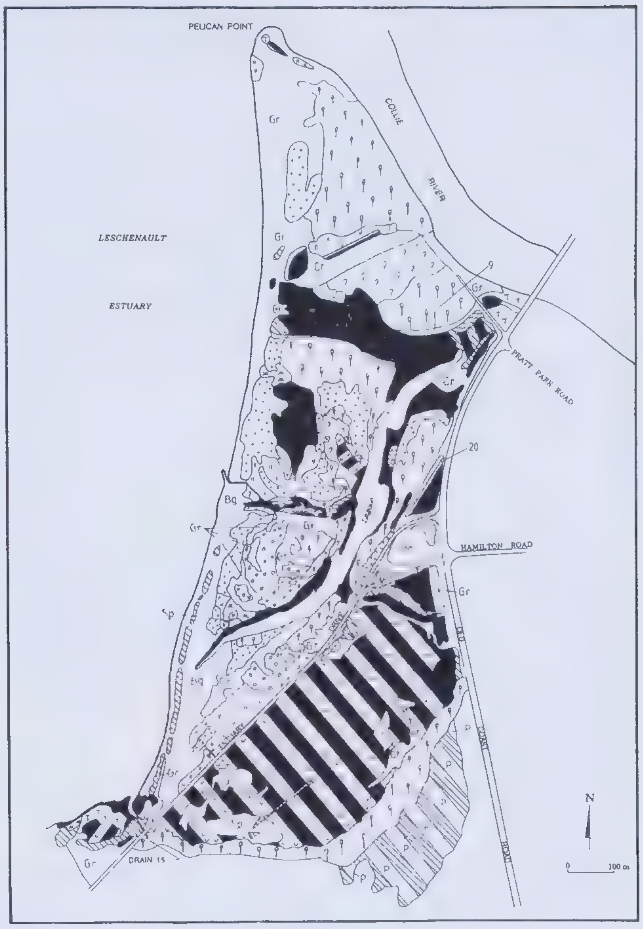


Figure 23. Collie River delta showing vegetation units.

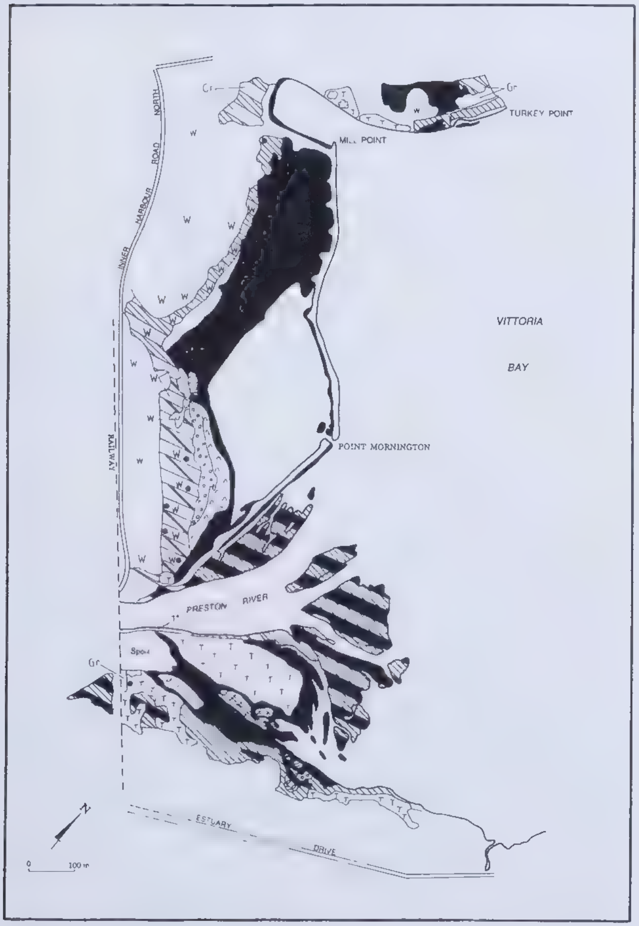


Figure 24. Southern estuarine shore showing vegetation units.

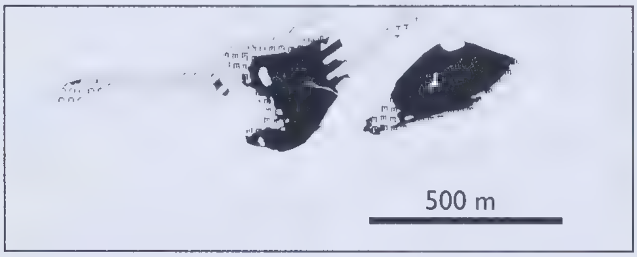


Figure 25. Detailed map of the Preston River delta showing vegetation units.

ence of the low decumbent samphire herb *S. quinqueflora*. These assemblages are:

Sarcocornia quinqueflora closed herbland: This is widely distributed around the estuary and basically forms extensive mats of samphire *S. quinqueflora*, either fringing the shoreline or behind a shoreline strip of sea rush *J. kraussii* closed rushland. The species seablite *Suaeda australis*, sea heath *Frankenia pauciflora*, streaked arrowgrass *Triglochin striata*, *Samolus repens* (a perennial small herb with no common name), *Halosarcia halocnemoides*, annual beardgrass *Polypogon monspelliensis*, saltwater couch *Sporobolus virginicus*, and sea rush *J. kraussii* can be common to sparse.

Suaeda australis - S. quinqueflora closed herbland: This assemblage is similar to the *S. quinqueflora* low closed herbland, except that seablite *Suaeda australis* is dominant.

Samolus repens-S. quinqueflora closed herbland: The small herb *S. repens* dominates this assemblage; it is found fringing with the *S. repens* closed herbland.

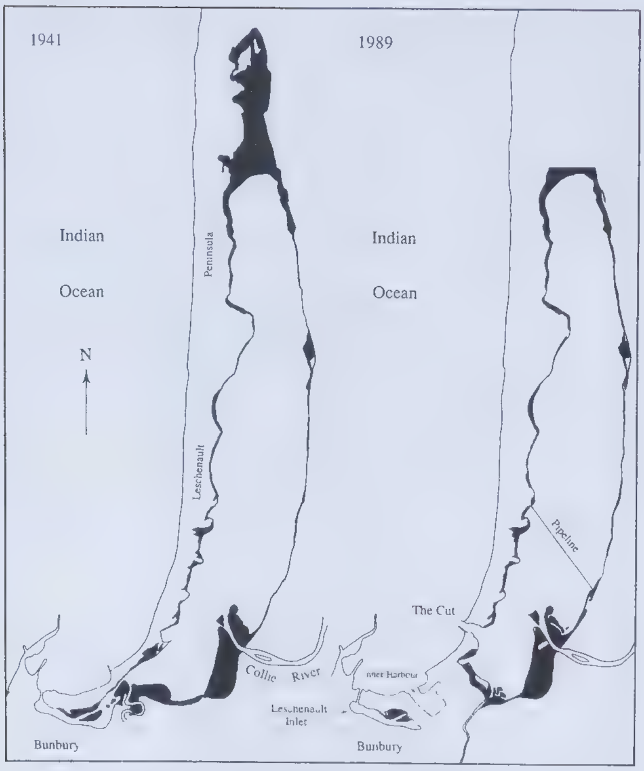


Figure 26. Extent of fringing vegetation along the Leschenault Estuary and the later Leschenault Inlet in 1941 and 1989.

Sarcocornia quinqueflora-Bolboschoenus caldwellii closed herbland: In a few localities the seasonal sedge club-rush *B. caldwellii* grows through the mats of samphire *S. quinqueflora* over the winter-spring period and then senesces.

Wilsonia humilis low open-closed herbland: *Wilsonia humilis*, a prostrate silvery decumbent herb, forms an assemblage with *S. quinqueflora* and *S. australis*, found only in the Sarcocornia complex on the remnant Preston River delta opposite the City of Bunbury.

Frankenia pauciflora-S. quinqueflora-S. australis low closed heath (*e.g.* Figs 22 and 24). Near the mouths of the Preston and Collie Rivers, seablite *Suaeda australis* and the samphire *S. quinqueflora* form a heathland of about 0.5-1 m high with the shrub sea heath *F. pauciflora*. Other species present include marsh saltbush *A. prostrata* and saltwater couch *S. virginicus*, and *Avicennia marina* and *Halosarcia halocnemoides* on the Preston River delta remnant.

Triglochin striata closed herbland. Trudgeon (1984) noted this assemblage along the Leschenault Peninsula, documenting it as a monospecific stand of the perennial herb streaked arrowgrass *Triglochin striata*. This herbland was not observed by Pen (1992). This assemblage may be considered a temporal phenomena that has no long term presence in any one site.

Samolus repens closed herbland. This consists of monospecific stands of the perennial herb *S. repens* and is found in small areas near the mouth of the Preston River (Fig 24) and in large patches along the western foreshore (Figs 9 and 11).

Sporobolus virginicus grassland. The perennial creeping grass saltwater couch *Sporobolus virginicus* sometimes forms extensive mats, occasionally with the samphire *S. quinqueflora* and saltwater couch *P. vaginatum*. Examples occur along the north-eastern corner of the estuary (Fig 12) and at Pelican Point (Fig 24).

Halosarcia halocnemoides low open heath. The shrubby samphire *Halosarcia halocnemoides* is a small shrub usually 20-30 cm in height, rarely reaching 1 m in height. It forms a low open heath in the most saline regions of the saltmarsh (Pen 1981), growing over the samphire *S. quinqueflora*, seablite *S. australis* and saltwater couch *S. virginicus*. Large stands of this assemblage are found at the northern end of the estuary (Fig 13) and formerly south of Old Coast Road near Pelican Point (Fig 23).

Halosarcia indica bidens low open heath. The shrubby *Halosarcia indica bidens* is a low shrub, usually 20-30 cm in height, reaching 2 m in height, forming an open heath in upper, saline parts of the saltmarsh (Pen 1981). On the Leschenault Inlet this assemblage also consists of the herbs seablite *S. australia* and marsh saltbush *A. prostrata*, the samphire *S. quinqueflora*, and the shrub sea heath *Frankenia pauciflora*. On Pelican Point the understorey of this assemblage also includes another samphire *Sarcocornia blackiana* and glasswort *Halosarcia syncarpa* (the latter species is found nowhere else in the study area, and the former only occasionally in other areas of the southern half of the estuary).

Gahnia trifida open sedgeland. Coastal saw sedge *Gahnia trifida* is a large tufted sedge which grows to 1.5 m, forming narrow bands on the fringe of saltmarsh between saline and relatively freshwater settings. It occurs within assemblages associated with more saline conditions and so has been classed as a marginal saltmarsh component. Stands are found at the north-eastern point of the estuary and at Pelican Point (Figs 13, 23).

Bolboshoenus caldwellii closed sedgeland. The native club-rush *Bolboshoenus caldwellii* is an ephemeral species which grows from rhizomes over the winter/spring period when salinities are low, and then subsequently senesces as salinities increase over summer and autumn. Small stands of this vegetation type are found along the Leschenault Peninsula (Trudgeon 1984), on the edge of pools or tidal lagoons. These stands were not of sufficient size for them to be consistently mapped, although occurrences of the species are marked on the maps where they have colonised stormwater-affected salt-marsh.

Fringing vegetation

Schoeneoplectus validus closed sedgeland. This tall weeping sedge which reaches 2 m, forms a small narrow monospecific stand near the north-eastern end of the estuary (Fig 15). The species often grows in shallow water and for this reason is referred to as emergent.

Paspalum vaginatum low closed grassland. The introduced creeping grass water couch *Paspalum vaginatum* occasionally forms monospecific low grassy mats on beaches (Figs 6, 7) and sometimes forms extensive mats near saltmarsh or fringing forest vegetation where the soil is waterlogged (Figs 8, 23). The species appears capable of tolerating the high salinities characteristic of the estuary.

Paspalum vaginatum-Bolboschoenus caldwellii closed grass and sedgeland. A significant stand of club-rush

Bolboschoenus caldwellii is present along the southern periphery of the Preston River mouth growing over a partially floating mat of salt water couch *Paspalum vaginatum*.

Fringing estuarine forest/scrub vegetation

Avicennia marina closed scrub or low closed forest. The white mangrove *Avicennia marina* forms stands of fringing forest in the Preston River delta area (which was once part of the narrow channel which connected the estuary to the ocean), and locally along the shore of the main Leschenault Inlet estuary. Isolated mangrove trees and shrubs are marked on the vegetation maps. The mangrove system is described in more detail in Semeniuk *et al.* (2000).

Melaleuca cuticularis low open-closed forest. The saltwater paperbark *Melaleuca cuticularis* is typically found on the saline soils bordering estuaries (Marchant *et al.* 1987), and on the Leschenault Inlet is mainly restricted to the northern part of the eastern foreshore (Figs 16 and 17). Here, it forms long and narrow bands of forest mostly to the landward of saltmarsh or fringing shoreline rushes. Only a small stand is found on the north-western corner. The understorey is mostly sea rush *J. kraussii*, *H. indica bidens*, samphire *S. quinqueflora*, seablite *S. australis*, saltwater couch *S. virginicus* and the tufted coastal saw sedge *G. trifida* are often present as are the introduced species wild aster *Aster subulatus*, marsh saltbush *A. prostrata*, couch *C. dactylon*, water couch *P. vaginatum* and dock *Rumex crispus*. The other small trees of the estuary, the swamp paperbark *M. rhaphiophylla* and saltwater sheoak *Casuarina obesa*, locally comprise part of the upper storey, as does the wattle coojong *Acacia saligna*.

Melaleuca rhaphiophylla-M. cuticularis low open forest. In one locality on the eastern foreshore, the swamp paperbark *Melaleuca rhaphiophylla* shares the upper storey with saltwater paperbark *M. cuticularis* forming a low open forest between sea rush *J. kraussii* and landward pasture. Understorey species are essentially the same as for the *M. cuticularis* low open-closed forest.

Melaleuca viminea low open to closed scrub. In saline sandy areas adjacent to saltmarsh or close to the foreshore, the small paperbark *Melaleuca viminea* forms an assemblage with a number of saltmarsh species occupying the understorey. They include *H. indica bidens*, samphire *S. quinqueflora*, seablite *S. australis*, sea rush *J. kraussii*, saltwater couch *Sporobolus virginicus*, coastal saw sedge *Gahnia trifida*, and sometimes sea heath *F. pauciflora*. *Melaleuca viminea* low open to closed scrub is found on the Collie River delta and locally along the eastern foreshore (Figs 17, 22 and 23).

Casuarina obesa low open - closed forest. The small saltwater sheoak *Casuarina obesa* forms a low open - closed forest over seablite *S. australis*, samphire *S. quinqueflora* and sea rush *J. kraussii* mostly in areas of the southern quarter of the estuary, especially along the river deltas and near "The Cut". Other species in the understorey include coastal saw sedge *G. trifida*, water couch *P. vaginatum* and sea heath *F. pauciflora*. *Casuarina obesa* also occurs with *M. viminea*, *S. virginicus*, *H. indica bidens*, *A. hypoleuca*, *W. humilis*, and *Hemichroa pentandra* on the remnant of the Preston River delta. This forest is often found along the shoreline (Figs 6, 7, 22-24).

Freshwater vegetation

***Baumea juncea* sedgeland.** To the landward of the *J. kraussii* closed sedgeland, which fringes the shoreline along most of the south-eastern shoreline, twig-rush *B. juncea* can be found fringing between the rush stand and the parkland grasses. Only seldom does it form a band of sufficient depth to enable its recognition as a separate vegetation unit. Unlike knotted club-rush *Isolepis nodosa* which is associated with sandy rises, twig-rush *B. juncea* is found in low lying areas associated with intermittent freshwater seepage. Such areas were probably favoured for clearing and pasture development in past years, and as a consequence little of the *B. juncea* closed sedgeland remains today.

***Melaleuca rhaphiophylla-Agonis flexuosa* low open-closed forest.** This assemblage, dominated by swamp paperbark and peppermint respectively, is found along the eastern shore (astride Cathedral Avenue in the vicinity of Crimp Crescent), either between high dry pasture or sandy rise vegetation and water logged pasture or between saltmarsh and the latter (Figs 16-18). The hydrologic setting suggests that this vegetation type is strongly associated with freshwater flushing from the landward side. Native understorey species such as coojong *A. saligna*, mat grass *Hemarthria uncinata*, jointed twig-rush *B. articulata*, common sword sedge *Lepidospermum longitudinale*, another tall sedge *L. gladiatum*, giant rush *Juncus pallidus* and twig-rush *B. juncea* which are typical of freshwater conditions, support this conclusion, but fringing estuarine species, including sea rush *J. kraussii*, knob sedge *Carex inversa* and coastal saw sedge *G. trifida* are also present. Numerous freshwater weeds may be present, including bridal creeper *Asparagus asparagoides*, soursob *Oxalis pes-caprae*, bracken fern *Pteridium aquilinum*, kikuyu *Pennisetum clandestinum*, an *Irridaceae* sp, arum lily *Zantedeschia aethiopica* and buffalo grass *Stenotaphrum secundatum*. This vegetation type is also found between saltmarsh, mainly *J. kraussii* closed sedgeland, and sand dune vegetation, chiefly *Agonis flexuosa* woodland to low open - closed forest, along the north-western foreshore (Figs 11 and 12). Here, members of the dune vegetation such as the shrubs *Spyridium globulosum*, *Acacia cochlearis* and cutleaf Hibbertia *Hibbertia cuneiformis*, are occasionally present, and weeds are far less common than on the eastern foreshore. Along the Leschenault Peninsula *M. rhaphiophylla-A. flexuosa* low open-closed forest is probably supported by freshwater seepage from the base of the sand dunes.

***Melaleuca rhaphiophylla* low open-closed forest.** In the Leschenault Inlet area, *Melaleuca rhaphiophylla* low open-closed forest occurs with an understorey of sea rush *J. kraussii* landward of the *J. kraussii* closed rushland. This is similar to its occurrence in some regions of the Swan River estuary where freshwater seepage is moderate. In the Leschenault Inlet area, the formation also occurs over samphire assemblages, or associated with *M. cuticularis* low open-closed forest (*e.g.* on the north-western foreshore; Figs 12 and 13). A small strip of this plant assemblage is found along the north-western foreshore along Cathedral Avenue.

Sandy rise vegetation

***Jacksonia furcellata* open-closed scrub**. This plant assemblage, dominated by the large shrub grey stinkwood *Jacksonia furcellata*, is found on sandy rises or small sand dunes located either along the beach front, as it was formerly in the Pelican Point area (Fig 23), or behind a band of fringing rushes of sea rush *J. kraussii* along the southern-eastern foreshore (Fig 21). Common understorey species included pigface *Carpobrotus edulis* and couch *Cynodon dactylon*. Less common species are the herb *Trachyandra divaricata*, harsh Hakea *Hakea prostrata*, coojong *A. saligna*, golden spray *Viminaria juncea*, saltwater couch *Sporobolus virginicus*, swamp paperbark *M. rhaphiophylla* and saltwater sheoak *C. obesa*.

***Eucalyptus rudis-Melaleuca rhaphiophylla* woodland**. The flooded gum *Eucalyptus rudis* locally forms a woodland with swamp paperbark *M. rhaphiophylla* (*e.g.* in the highest parts of Point Douro and Pelican Point and in some areas north and south of the estuary; Figs 22 and 23). The understorey of this vegetation type has been depleted of native species, probably as a result of frequent fire and weed invasion. Mostly it consists of perennial veldt grass *Ehrharta calycina* and the herb *Trachyandra divaricata* along with a plethora of other weeds. Only some native species including grey stinkwood *Jacksonia furcellata*, common sword sedge *Lepidosperma longitudinale*, sea rush *J. kraussii* and knotted club-rush *I. nodosa*, remain today. In some adjacent areas the understorey has been completely replaced by lawn or parkland development and only the relic flooded gum *E. rudis* trees remain.

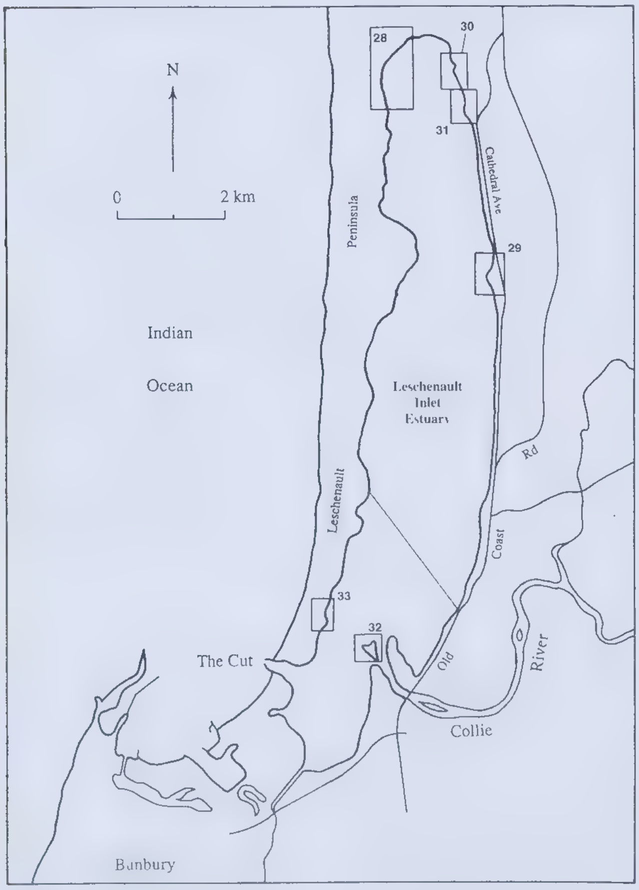


Figure 27. Location of sites where vegetation changes and one landform change have been documented.

***Acacia saligna* low closed forest**. Along the north-eastern foreshore the small tree coojong *Acacia saligna* is very common. Here it has invaded the native plant assemblages, pasture and road verges, probably as a result of frequent fires which favour many *Acacia* species. In places these occurrences are so dense that the species forms a low closed forest (*e.g.* just north of Crimp Crescent on the eastern foreshore; Fig 17).

***Juncus kraussii-Isolepis nodosa* low closed sedgeland**. Where the foreshore abuts a sand dune, as is often the case along the south-western side of the estuary, or a sandy rise, which is more commonly the case along the eastern foreshore, the knotted club-rush *Isolepis nodosa* often occurs to landward of the *J. kraussii* closed rushland. Along the western foreshore, this formation often merges with sand dune species such as red-eyed wattle *Acacia cyclops*, the large shrub *A. cochlearis*, coast daisy bush *Olearia axilaris* and cutleaf hibbertia *Hibbertia cuneiformis*. Along the eastern foreshore much of the native vegetation on the landward side of the sea rush *J. kraussii* has been cleared and replaced with parkland and consequently *J kraussii-I. nodosa* low closed sedgeland is present only as a remnant narrow strip bordering lawn.

Freshwater vegetation (forest and disturbance-related assemblages)

The chaotic plant assemblage. Over large areas of Pelican Point up until the mid 1990s the vegetation was too heterogeneous to enable the recognition of definite plant assemblages (Fig 23). A wide area of native and introduced species typical of saline and freshwater environments and a large range of weeds were present. The more successful species include swamp paperbark *M. rhaphiophylla*, paperbark *M. viminea*, sea rush *J. kraussii*, samphire *S. quinqueflora*, seablite *S. australis*, coastal saw sedge *G. trifida*, flooded gum *E. rudis*, marsh saltbush *A. prostrata*, rye grass species *Lolium* spp., water couch *P. vaginatum* and couch *C. dactylon*. It would appear that these areas were in a state of flux, probably brought about by a combination of factors including frequent fires, physical disturbance (as indicated by the irregularity of the ground surface) and frequent alteration to the salinity/freshwater flushing regime caused by the Cut, drains, nearby reclamation, and the construction of Taylor Road. Note that this area has now been developed.

***Melaleuca rhaphiophylla* low closed (swamp) forest**. Swamp paperbark *Melaleuca rhaphiophylla* forms patchy stands of closed forest over small lakes in north-eastern region of the study area (Fig 14).

Pastured woodlands. In some areas of the eastern and southern foreshores relic trees from past stands of forest and woodland assemblages remain over parkland or pasture grasses. A small stand of saltwater sheoak *C. obesa* trees over parkland can be found near Mill Point where it abuts a stand of *C. obesa* low open forest (Fig 24). A large area of

M. rhaphiophylla-A. flexuosa pastured woodland is found on the central eastern foreshore from Australind Road to the base of the ridge line (Fig 16). This suggests that the *M. rhaphiophylla-A. flexuosa* low open-closed forest was once far more extensive along the Leschenault Inlet than it is today. Peppermint (*Agonis flexuosa*) woodland is also found in the area but only in small patches (Fig 21). Flooded gum *Eucalyptus rudis* pastured woodland, probably representing the relic trees of the *E. rudis-M. rhaphiophylla* woodland, is found on Point Douro and to the north of the pipeline (Figs 20 and 22). In the most north-eastern corner of the study area *Eucalyptus gomphocephala* (tuart)-*A. flexuosa* and *E. gomphocephala* pastured woodlands are found over relatively broad pastured areas.

Vegetation changes since 1941

There have been some marked changes in the peripheral vegetation of the Leschenault Inlet estuary evident in the aerial photographs taken since 1941 (Figs 27-33). Fig 27 shows location of more detailed maps. Figs 28-33 show detailed maps of vegetation changes. Some of the changes have occurred in the vegetation alone, without changes in the habitats, and some have been induced by changes in estuarine coastal landforms. These are described in the following sections: 1. clearing of fringing vegetation; 2. decline of estuarine fringing forest; 3. encroachment of *J. kraussii* into the estuary; 4. colonisation of river deltas; 5) formation of tidal lagoons or pools along the high tidal platforms; and 6) weed invasions.

Clearing of fringing vegetation

The extent of fringing vegetation, in 1941, comprised some 700 ha of which about 350 ha remained in 1989 (Fig 26). Since this time, most of the remnant fringing forest and newly formed saltmarsh on Pelican Point has been destroyed by development. Large areas of samphire which colonised dredging spoil and artificial lagoons along the southern end of the estuary also have been destroyed by harbour development.

Further substantial losses of fringing vegetation have occurred to the north of Buffalo Road through clearing and drainage for agriculture, with loss of glasswort *H. halocnemoides* low closed heath and fringing forests of most probably saltwater paperbark (*M. cuticularis*), swamp paperbark (*M. rhaphiophylla*) and peppermint (*A. flexuosa*), and to the south where large areas, including most of the original estuary mouth, have been reclaimed for harbour construction. Much of the narrow strip of fringing vegetation along the eastern foreshore also has been cleared on the landward side corresponding to the elevated stranded platform, leaving an even narrower strip today. However, along the western shore of the Leschenault Inlet estuary foreshore, the narrow band of fringing vegetation remains largely intact.

Relic trees present over pastured floodplain to the east of Cathedral Avenue and south of Buffalo Road, and corresponding to the elevated platform, indicate that these areas once supported swamp paperbark *M. rhaphiophylla* low closed forest, *M. rhaphiophylla- A. flexuosa* low closed forest, and forests and woodlands dominated by tuart *E.*

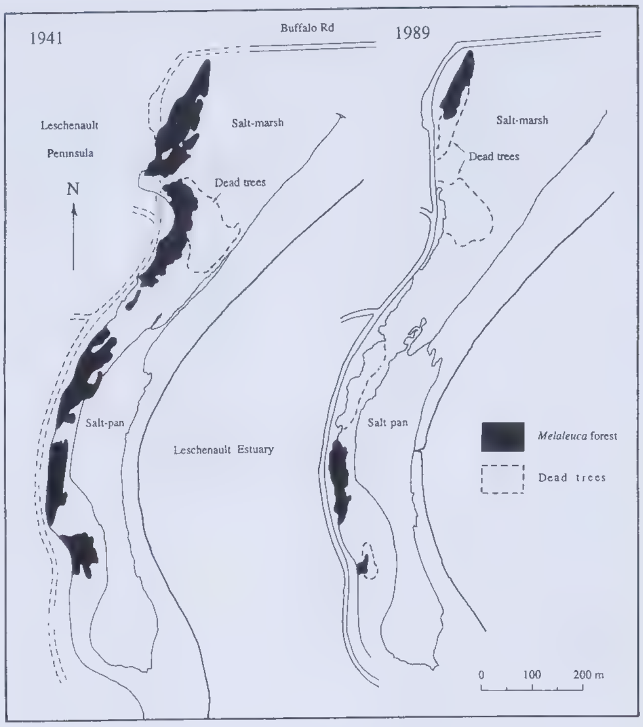


Figure 28. The extent of Melaleuca dominated forest in 1941 and 1989 in the north-western corner of the Leschenault Inlet.

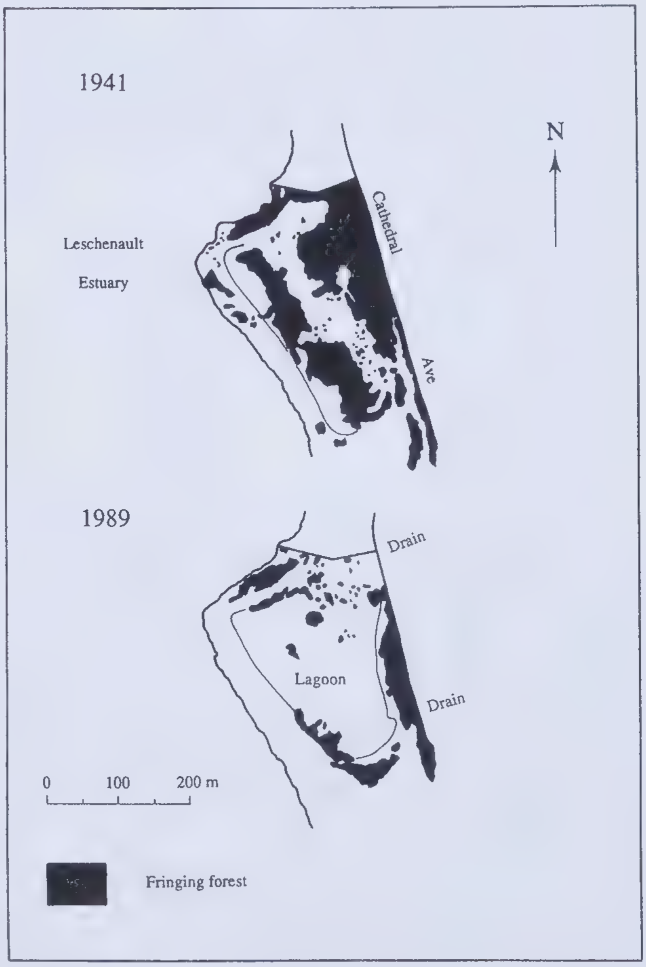


Figure 29. The extent of fringing forest in 1941 and 1989 around and on a tidal lagoon on the eastern foreshore of the Leschenault Estuary.

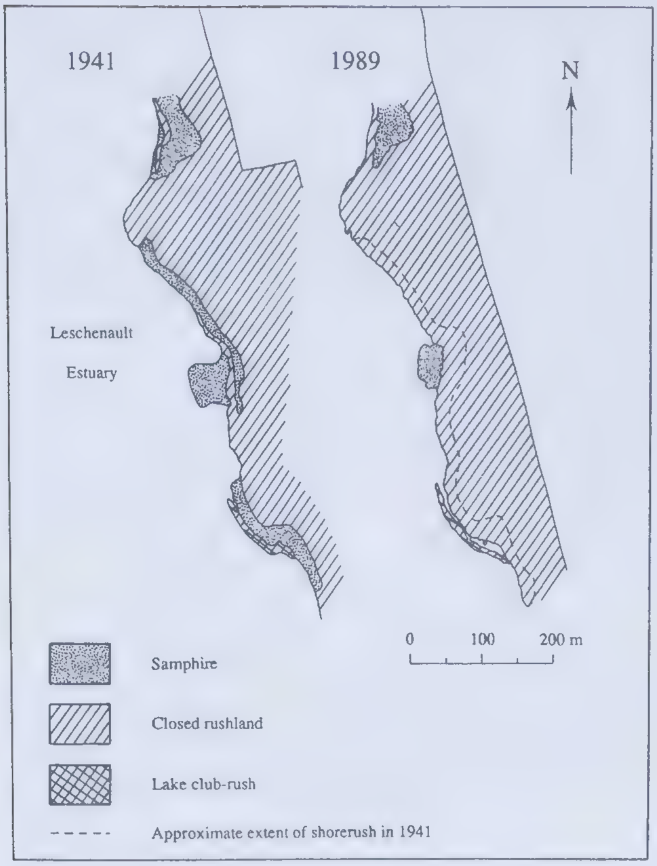


Figure 30. Extent of closed rushland and lake club-rush (*Schoenoplectus validus*) in 1941 and 1989 in a region of the north-eastern foreshore of the Leschenault Estuary.

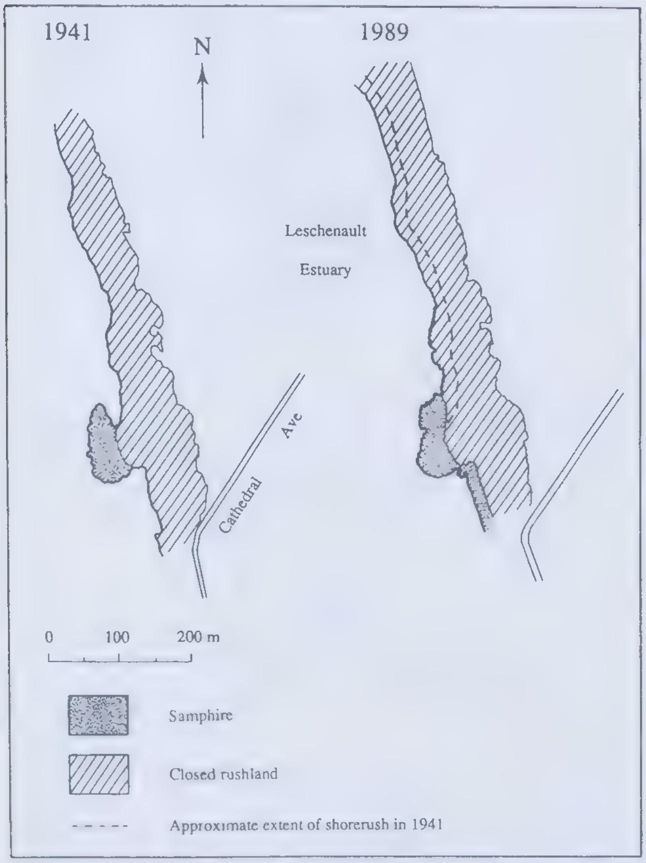


Figure 31. Extent of samphire and closed rushland in 1941 and 1989 along a region of the north-eastern foreshore of the Leschenault Estuary.

gomphocephala and/or peppermint *A. flexuosa*. The parkland areas near Australind and Point Douro today support relic flooded gum *E. rudis*, suggesting that these areas once supported stands of *E. rudis-M. rhaphiophylla* forest.

Decline of estuarine fringing forest

Prior to the development of the south-eastern corner of the estuary, the most marked decline in fringing forest was in the central area of Pelican Point (Figs 28 and 29). Fringing forests of paperbarks have been replaced by saltmarsh and the chaotic plant assemblage. This change has probably brought about by alteration to drainage patterns in the area as part of urban development. The effect has been to shift the salinity/freshwater balance in the direction of increasing salinity, favouring saltmarsh at the expense of fringing forest.

A decline in fringing forest to the north-east of the estuary (Fig 28), particularly of saltwater paperbark *M. cuticularis* and swamp paperbark *M. rhaphiophylla* had already occurred before 1941 (white tree trunks evident in aerial photographs, and confirmed by field observations of dead and dying trees). As this decline predates "The Cut" and no alteration to the drainage of the area is obvious, it is difficult to explain. If a local increase in salinity had been the cause, the nearby salt-pans, where salinity levels are at an extreme and preclude all fringing plant growth, would have increased in size, however, they have largely remained unaltered since 1941.

The death of fringing forest in the lagoon area north of Crimp Crescent is probably due to a general increase in salinity brought about by artificial drainage (Fig 29). This is also indicated by the death of *J. kraussii* (which probably once formed the understorey of the forest), and its replacement by samphire species and by a stand of Bullrush (*Typha orientalis*) in one corner of the lagoon. The replacement of *J. kraussii* by samphire indicates a recent increase in salinity while the bulrush encroachment suggests localised freshwater flushing caused by artificial drainage of the adjacent waterlogged pastures. In other words, a steady year long flushing of the lagoon area by groundwater has been replaced by more centralised drainage, causing an increase in salinity over most of the area and a decrease in salinity in specific areas, probably at certain times of the year only.

However, there is some evidence of recent fringing forest regeneration. Near Crimp Crescent a small stand of *M. viminea* low open-closed forest (Fig 17), which is associated with very saline conditions, has been slowly growing in size since at least 1941. Further, the presence of young trees of swamp paperbark (*M. rhaphiophylla*), *M. viminea* and saltwater paperbark (*M. cuticularis*) indicate a resurgence of fringing forest in some parts of Pelican Point.

Encroachment of *Juncus kraussii* closed rushland

In most areas of the estuary where the foreshore is fringed with *J. kraussii*, the species is encroaching into the estuary, and moving across samphire flats, beach sands, or the sandy estuarine substrate. Considerable encroachment into the estuary is evident at four locations (Figs 30 and 31), and aerial photographic evidence suggests an encroachment rate of 5-20 m over the last 50 years. On site, this encroachment is evident by the growth of rhizomes with tapering leaf height, the smaller leaves being present at the growing end of the rhizome.

This estuary-ward encroachment of fringing sedges and rushes may have been caused by a reduction in mean water level over the winter months as a result of the construction of "The Cut". Several field observations support this. Firstly, *J. kraussii* occurs at two levels along the estuary shore: near estuarine waters it resides at a much lower level than to landward, indicating together with other observations, recent growth has occurred at a distinctly lower level. Secondly, there has been erosion and subsequent undermining of *J. kraussiii* along the south-western foreshore near "The Cut"; here, the 10-20 cm deep rich organic matter and root-mesh layer which supports *J. kraussii* is being undermined as waves or currents wash away the underlying sandy substrate. Locally, *J. kraussii* has established in front of the erosional cliff. In general, it would appear that a reduction in mean estuarine water level increased the exposure of an area of sandy substrate, and subsequently waves at low tide and possibly currents at high tide eroded the substrate eventually exposing and undermining the peat layer of the sedgeland. Concomitantly, reduced water level enabled *J. kraussii* to become established, probably vegetatively, at a lower level of the estuary in front of the site of erosion. In other parts of the estuary, free of erosion, *J. kraussii* simply colonised the new lower tidal sites which had become favourable for growth. If the encroachment is due to the effects of "The Cut", then it has occurred since 1951, suggesting an encroachment rate of 5-20 m over the past 40 years.

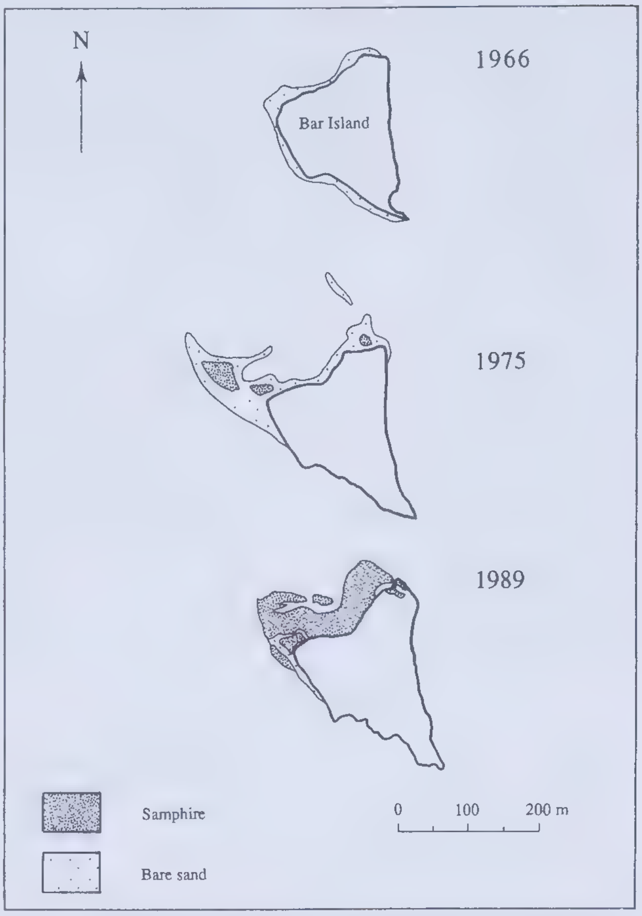


Figure 32. Colonisation of bare sand by samphire from 1966 to 1989 on Bar Island.

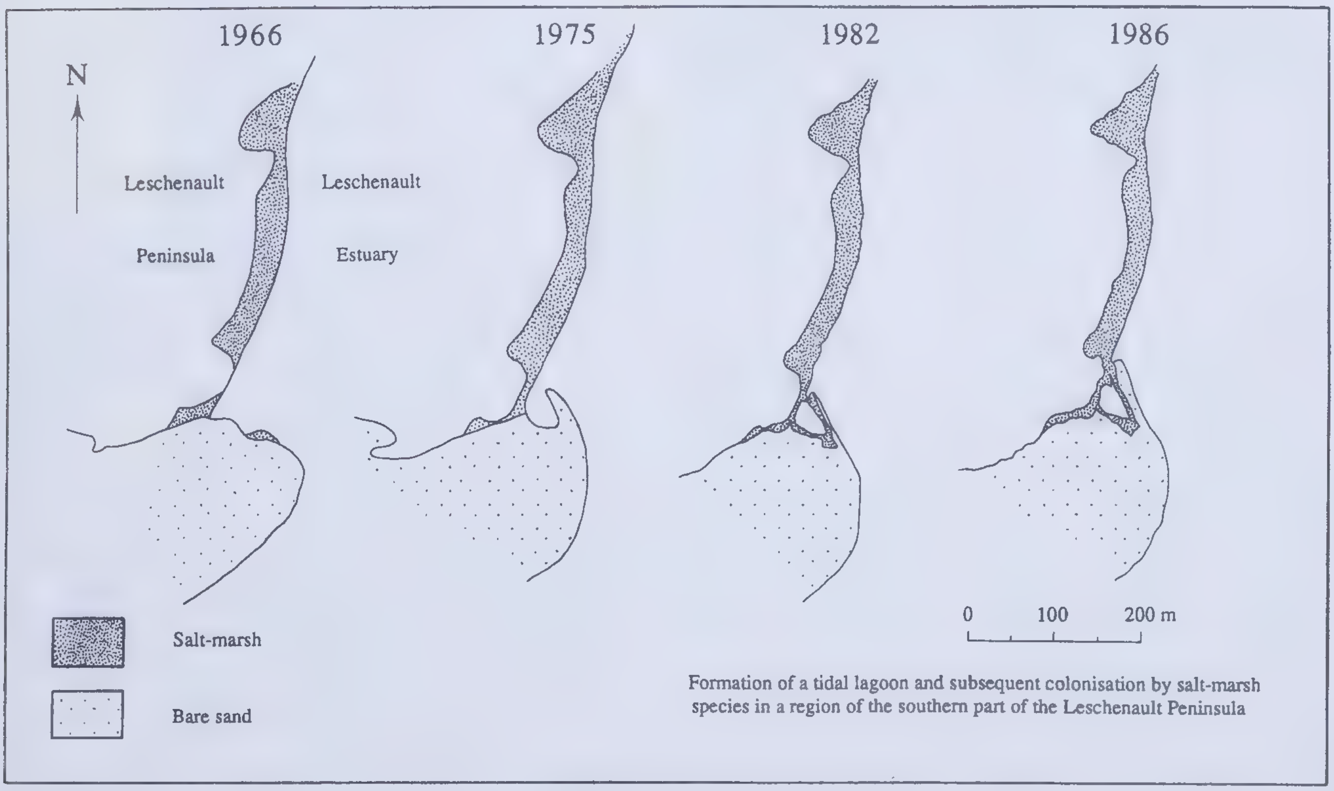

1966
1975
1982
1986
N
Leschenault
Peninsula
Leschenault
Estuary
Salt-marsh
Bare sand
0
100
200 m
Formation of a tidal lagoon and subsequent colonisation by salt-marsh species in a region of the southern part of the Leschenault Peninsula

Figure 33. Formation of a tidal lagoon and subsequent colonisation by saltmarsh species in a region of the southern part of Leschenault Peninsula.

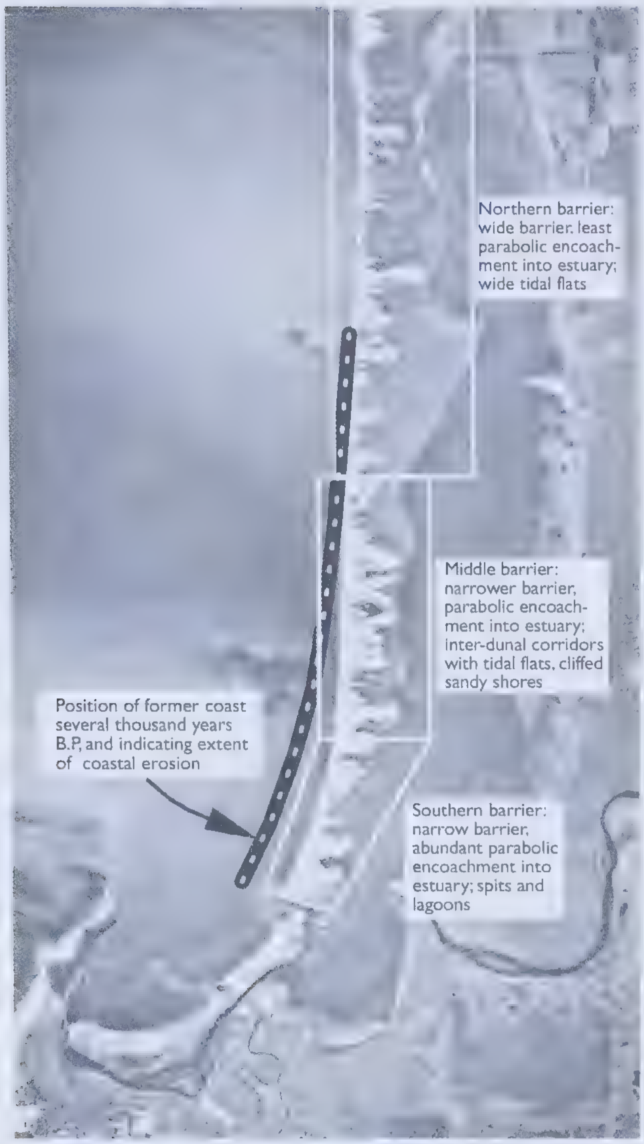

Northern barrier: wide barrier. least parabolic encoachment into estuary; wide tidal flats
Middle barrier: narrower barrier, parabolic encoachment into estuary; inter-dunal corridors with tidal flats, cliffed sandy shores
Position of former coast several thousand years B.P, and indicating extent of coastal erosion
Southern barrier: narrow barrier, abundant parabolic encoachment into estuary; spits and lagoons

Figure 34. The various sectors along the Leschenault Peninsula showing south to north variation in erosion of the barrier, and its effect on parabolic dunes encroaching into the estuary.

Colonisation of river deltas

The colonisation of recently deposited river sediments by fringing estuarine vegetation can be rapid (Pen 1981). Colonisation by samphire of the sandy deposits at the north-western end of the mid-channel island at the mouth of the Collie River delta has largely occurred since 1975 (Fig 32). More extensive colonisation by fringing vegetation occurred on the recently formed artificial Preston River delta (now removed) and the enclosed mud-flats at Point Mornington. In these areas *Sarcocornia quinqueflora* complex and *J. kraussii* closed sedgeland completely colonised the low-lying mud flats over a ten-year period from 1977 and presently *Casuarina obesa* low open forest has developed on the high central area on the east bank.

Tidal lagoons/pools along high tidal platforms

Along the southern foreshore of the Leschenault Peninsula there are a number of small tidal lagoons or pools. These have formed by encroachment of parabolic dunes, followed by dune tip erosion by currents moving in a north to north-west direction causing the formation of a sand bar which entraps a body of water within a roughly triangular shaped area (Fig 33). Over the years, fringing vegetation colonised this area and gradually encroached upon the pool, and eventually, through the accretion of aeolian sand and organic matter, fringing vegetation colonised the entire area, forming a small triangular shaped saltmarsh. There are many examples of such areas along the southern half of the Peninsula.

As the bar-and-lagoon systems evolve from barred water bodies to gradually infilling lagoon, the vegetation assemblage changes. There is a progressive change from sand-filled lagoon barred by a sandy spit, to a sand, muddy sand and organic matter-filled lagoon to a sand and organic matter-filled emergent wetland. The vegetation that progressively inhabits these lagoons is zoned in response to salinity gradients, and in response to the amount of freshwater that seeps into the system from the adjoining dunes. The sequence of vegetation development is summarised below as bar-and-lagoon stages 1-3 in terms of the stage of development of bar-and-lagoon, the sediment fills and salinity gradients, and the types of vegetation developed. During stage 1, the bar-and-lagoon is an aquatic lagoon, barred by a spit. Its substrate is sand and muddy sand, remnant from tidal and subtidal environments of an inter-parabolic dune corridor. It is inhabited by *Ruppia*, or similar aquatic macrophyte, in subtidal environments.The saline margins are inhabited by Sarcocornia and *J. kraussii*. Sandy rise vegetation inhabits the spit or bar. During stage 2 the bar-and-lagoon is a seasonally inundated basin. Aeolian sand, and organic matter continue to fill the basin. There is saline water recharge from the estuary, and locally freshwater seepage from the dunes. The basin is inhabited by zoned vegetation: central parts of the basin are inhabited by samphire such as Sarcocornia, and Halosarcia, and upper parts of basins are inhabited by *Juncus kraussii* and *Casuarina obesa*, or where there is significant freshwater seepage by *Melaleuca rhaphiophylla*. Sandy rise vegetation inhabits the spit or bar. During stage 3, the bar-and-lagoon system is an emergent wetland basin. Aeolian sand and organic matter continue to fill the basin. There is saline water recharge from the estuary, or locally freshwater seepage from the dunes. The central basin is covered by *J. kraussi*, with *M. rhaphiophylla* over *J. kraussii* and *I. nodosus* to landward (if dominated by freshwater seepage), or by *M. cuticularis* (if there is reduced freshwater seepage), or by *C. obesa* (if estuarine water recharge dominates the hydrology). Sandy rise vegetation inhabits the spit or bar.

Weed invasions

The main weeds and alien species invading and replacing estuarine shoreline vegetation include couch *Cynodon dactylon*, kikuyu *Pennisetum clandestinum*, salt water couch *Paspalum vaginatum*, buffalo grass *Stenotaphrum secundatum*, pigface *Carpobrotus edulis*, coojong *Acacia saligna*, Bullrush *Typha orientalis*, and club rush *Bolboschoenus caldwellii*.

The most significant weed invasion along the shore of the estuary is in fringing *Juncus kraussii* formations. For

Table 2. Variation of barrier, shore types, habitat and gradients north-south along the Leschenault Peninsula, and its effect on the parabolic dune influenced estuarine shore

Location along barrier	Description of barrier, and extent of oceanic erosion	Shore types developed along estuary margin	Habitats and groundwater dynamics
northern barrier	wide barrier, least seaward face erosion, and hence fewer parabolic dunes encroaching into estuary	broad tidal flats, with mud derived from tidally deposited northward-drift transported suspended mud	mud flats, estuary source water recharge and evaporation to develop hypersaline fields; little effect of freshwater seepage from barrier dunes
middle barrier	narrower barrier, more seaward face erosion, and hence more abundant parabolic dunes encroaching into estuary	shore line dominated by parabolic dunes with broad intervening tidal flats and embayments in inter-dune corridors; mud derived from reworking of platforms, is deposited tidally in corridors, alternating with cliffed dunes where estuarine erosion is incising into the shores	mud flats between dune fingers/ridges; estuary-source water recharge and evaporation to develop hypersaline fields; effects of freshwater seepage from barrier dunes along interfaces between dunes and tidal flats
southern barrier	narrowest part of barrier, in the zone of the most extreme seaward face erosion, and hence most abundant parabolic dunes encroaching into estuary	shore line dominated by active parabolic dunes, and cliffed parabolic dunes, with spits, bars and lagoons; small intervening lagoons, tidal flats and embayments in inter-dune corridors; mud is deposited tidally in corridors	embayments and mud flats between dune fingers/ridges, barred by spits derived from dune tips; the zone of the most complex groundwater hydrodynamics, with dunes, spits/bars, and mudflats exerting influence on groundwater from estuary-sources, rainfall, and dune groundwater seepage. Because of abundance and proximity of parabolic dunes, and direct control of dunes on coastal landforms, this area exhibits maximum effects of freshwater seepage on coastal vegetation

instance, along the south-eastern foreshore, grasses and other weeds are invading from the adjacent parkland into the landward side of the narrow shoreline closed sedgeland of *J. kraussii*. The common weeds are couch, kikuyu, water couch, buffalo grass and pigface. The shoreward edge of the sedgeland remains relatively free of weeds, although water couch often forms mats on areas of exposed sand. A reduction in mean water level brought about by "The Cut" together with the clearing of native vegetation behind the *J. kraussii* strip and its subsequent replacement by grasses and other weeds provide explanations for this invasion. A reduction in mean water level would not only mean that *J. kraussii* could encroach upon the estuary but that the vegetation assemblages, probably dominated by twig-rush *B. juncea*, knotted club-rush *I. nodosa* and swamp paperbark *M. rhaphiophylla* could have encroached upon the *J. kraussii* assemblage. However, these landward assemblages, having been replaced by grasses and other weeds, have not been present to respond to the change in environmental conditions. Instead the weeds have responded and are slowly invading and replacing the *J. kraussii* zone.

The small tree and native weed coojong is colonising successfully along the north-eastern foreshore of Leschenault Inlet, where it is favoured by frequent fires (Pen 1992). It is a common member of freshwater fringing forest assemblages and has formed dense stands in some areas.

Bullrush and native club rush locally are colonising the estuary shore, but while elsewhere these species are abundant along the Swan-Canning River Estuary, either fringing the rivers or invading the saltmarshes receiving additional channelled stormwater input, their effect in Leschenault Inlet is as yet minor. Bullrush is present in some localities receiving freshwater via drains or freshwater seepage at the base of dunes. Club-rush is found in a few localities fringing tidal pools and along the Preston River. The distribution of these two species is limited to localised reductions in salinity, and thus neither presently represents a major threat to native plant assemblages.

Paspalum vaginatum forms extensive grassy mats on beach sand and narrow mats in and about *J. kraussii* on the immediate foreshore in some areas. Along the Preston River it forms dense partially floating mats and may be found in association with club-rush *Bolboschoenus*. Although alien, it helps to stabilise the foreshore and does not appear to prevent the colonisation or regeneration of native species. However, landward of the foreshore it can be an invasive species contributing to the replacement of *J. kraussii* on higher and dryer ground. It can also form dense mats in areas of saltmarsh receiving freshwater input, but its status as an invader in these circumstances is uncertain and requires further investigation.

The climber bridal creeper *Asparagus asparagoides* is abundant in the low open closed forest assemblage of *Melaleuca rhaphiophylla* and *Agonis flexuosa* north of Crimp Crescent. Elsewhere, outside of Leschenault Inlet (*e.g.* the Canning River), this species is a troublesome weed and has the capacity to smother native shrubs and juvenile trees, and so must be regarded as a potential threat to this assemblage.

Shoreline vegetation, geomorphic setting and salinity

There appear to be four determinants controlling the extent and type of saltmarsh present along the shore. The two most important two influences are geomorphic setting and physical estuarine coastal processes. The third is a south to north gradient in source water salinity, and the fourth is anthropogenic effects.

At the largest scale, the Leschenault Inlet estuary has several shore settings as habitats for peripheral vegetation; geomorphic context and groundwater settings are the main formative processes. The habitat settings are: 1) the eastern shore of the estuary, developed as a laterally consistent sand platform and shore, cut into the Mandurah-Eaton Ridge, provides a relatively consistent shore habitat in terms of coastal landforms, substrates, and estuary-derived and hinterland-derived groundwater hydrodynamics; 2) the digitate delta of the Collie River, with an array of heterogeneous habitats, reflecting heterogeneity of intra-deltaic landforms, substrates, and groundwater systems; 3) the tidally-influenced delta of the Preston River, with an array of heterogeneous habitats, also reflecting heterogeneity of intra-deltaic landforms, substrates, and groundwater systems; and 4) the western to northern shore of the estuary, with a south to north heterogeneous array of coast types, reflecting large scale variation in abundance of parabolic dunes reaching the shore of the estuary. This variation results in a south to north variability in coastal landforms, coastal processes, substrates, and effects of tidal zone groundwater hydrodynamics and dune-derived fresh water seepage, as described below.

The barrier of the Leschenault Peninsula is rapidly eroding (Semeniuk & Searle 1987), with an erosion rate of up to 1 m annually. In the longer term, over the latter part of the Holocene, there has been a variation in the rate over the length of the Peninsula, with the most marked erosion occurring in southern parts, and less erosion in northern parts of the barrier. As a result, the barrier is narrower to the south. The dynamics of this south to north variation, and its effect on parabolic dunes encroaching on the estuary, is summarised in Table 2. and in Fig 34.

The third determinant, estuarine source water for the tidal flats has a subtle effect on vegetation type in a south to north gradient along the shore of the estuary. The main part of the tidal zones is recharged by estuarine water. Thereafter, once emplaced, the near-surface groundwater and soilwater are subject to evaporation, or dilution by meteoric recharge. In this context, given that there is a similar evaporative field across the tidal flats from north to south induced by solar radiation and by wind, and a similar influx of meteoric water, any variation of groundwater and soilwater salinity may be expected to be primarily determined by the salinity of the source water. As noted earlier, Wurm & Semeniuk (2000) describe four fields in the salinity of the aquatic portion of the estuary: 1) a marine to hypersaline northern portion; 2) a large marine central portion; 3) a marine to brackish southern portion; and 4) a deltaic portion. These various source water salinities have the potential to influence the salinity of upper tidal groundwater and soilwater.

The best location to unravel the effects of estuarine source water salinity variation is the eastern estuary shore. Here, at the large scale, there is not the south to north habitat variation, and hence the shore could be viewed as exhibiting a consistency of habitat within which south to north groundwater variability may be expressed by vegetation composition and structural variation. However, anthropogenic effects are more prevalent and impact on the shore vegetation. Nonetheless, in our estimation, recognising from site to site the effects of anthropogenic activities on coastal vegetation in terms of salinity changes and vegetation changes (as described above in an earlier section of this paper), there appears to be a south to north variation in composition of saltmarsh vegetation reflecting the source water salinity variation. These patterns of saltmarsh type in relation to regional salinity fields are summarised as follows: 1) in the southern part of the estuary, where estuarine waters are marine to brackish, the shore vegetation is dominated by *J. kraussii*; 2) in the middle part of the estuary, where estuarine waters are mainly marine water, the shore vegetation is dominated by *J. kraussii*; and 3) in the upper part of the estuary, where estuarine wasters are marine to hypersaline, the shore vegetation is dominated by *S. quinqueflora*.

The fourth determinant is anthropogenic, relating to the effects of altered drainage, and groundwater hydrodynamics brought about by draining, clearing, dewatering, urbanisation, dredging and spoil disposal, and road construction. These effects variably and locally have changed the recharge dynamics, discharge dynamics, and salinity of coastal habitats, resulting in the changes in assemblage composition, and mortality of some species.

It is difficult to disentangle the effects of habitat variation and source water salinity to explain the distribution of saltmarsh vegetation in a south to north gradient along the western Leschenault Inlet estuarine shore, from a perspective of natural dynamics alone, since anthropogenic effects here are at a minimum. What may be viewed as an increase in salt-tolerant species from south to north, perhaps reflecting the south to north variation in salinity of estuarine source water, may also be viewed as a reflection of the greater development and availability of mud-floored tidal flats, and the diminishing effect of freshwater seepage from neighbouring dunes. The complexity of the inter-relationship of gradients in coastal landforms, their internal groundwater dynamics, and effects of a variable estuarine source water salinity, however, must await further study.

Comparison with other estuaries:

The Leschenault Inlet estuary and its peripheral habitats and vegetation are briefly compared with five other estuaries and peripheral vegetation along the south-western and southern coast in terms of landform setting, heterogeneity of coastal landforms and peripheral vegetation habitats (Table 3), peripheral vegetation species composition, and diversity of vegetation assemblages (Table 4). The estuaries and coastal systems considered in this comparison are: Swan-Canning Estuary; Peel-Harvey estuary; Walpole-Nornalup estuary; Princess Royal Harbour; and Oyster Harbour. These results suggest the following ranking of estuaries in terms of the richness of their peripheral vegetation associations (the number grading is derived from Table 4 with 20 the highest, and 10 the least significant): Leschenault Inlet estuary (20); Walpole-Nornalup Inlet (20); Swan River estuary (17); Princess Royal Harbour (16); Oyster Harbour (16); and Peel-Harvey estuary (10).

Discussion

The Leschenault Inlet estuary presents a heterogeneous array of shore habitats, resulting from a variable upland geomorphic setting (*i.e.* the south to north gradient along the west coast, and east-coast *vs* west-coast *vs* north-coast setting), the variable coastal processes operating on the coast (to generate progradational mud flats *vs* cliffed dune shores *vs* bar-and-lagoon complexes *vs* tidal platforms), upland to estuarine groundwater hydrodynamics and interactions, deltaic build-up at river mouths, and a complex sealevel history to develop stranded estuarine landforms. In contrast, its subtidal habitats are relatively simple and extensive. In a State-wide perspective, the array of peripheral and aquatic habitats are exclusive to Leschenault Inlet, with this system being the only estuarine lagoon in Western Australia situated leeward of a retreating dune barrier. As such, the complex array of estuarine coastal landforms and peripheral vegetation habitats are regionally significant, notwithstanding that some of the vegetation assemblages are regionally widely distributed.

Table 3. Comparison between geomorphic setting and peripheral estuarine habitats of the main south-western and southern estuaries

Estuary	landform setting and processes	heterogeneity of coastal landforms and peripheral vegetation habitats
Swan-Canning Estuary	inundated valley tract of the Swan and Canning Rivers, traversing a range of coastal plain geomorphic units	the shores are mainly erosional forms cut into limestone or sand, with local depositional nodes such as beachridges on meanders; thus, small scale habitats are sandy beaches, small barred lagoons, limestone cliffs, mud and muddy sand platforms
Peel-Harvey estuary	located at junction between limestone ridge and Bassendean Dune terrain	range of complex shore types dependent on location within the estuary (Semeniuk & Semeniuk 1990): modern and stranded tidal deltas, stranded sand flats, limestone cliff shores, spits and lagoons, beaches, fluvial deltas
Leschenault Inlet estuary	located behind high Holocene dune barrier, and encroaching on high sandy Mandurah-Eaton Ridge	range of complex shore types dependent on location within the estuary (this paper), related to east-coast *vs* west coast *vs* north coast settings, and in relationship to encroaching dunes: high tidal platforms, bar-and-lagoon complexes, beaches, cliffed dune shores, deltas
Walpole-Nornalup Inlet estuary	located in inundated hilly terrain of Precambrian rock, and barred by a Holocene dune barrier	peripheral habitats related to edge of stable dune barrier, deltas, and the steep slopes cut into Precambrian bedrock; habitats include: narrow tidal flats, beaches, delta landforms, rocky shores
Princess Royal Harbour	located in inundated hilly terrain of Precambrian rock, barred by barrier dune, and tombolo	peripheral habitats related to edge of granitic/saprolitic hills, edges of sand dune barrier and tomboloes, and fluvial lowlands; habitats include sandy beaches, tidal flats, small barred lagoons
Oyster Harbour	located in inundated hilly terrain of Precambrian rock and undulating sand plain	peripheral habitats related to edge of granitic/saprolitic hills, reworked edge of an undulating sand plain, and deltaic landforms; habitats include sandy beaches, tidal flats, small barred lagoons, deltaic systems

Table 4. Dominant native fringing plant species of selected south-western and southern estuaries

Species	Swan (Pen 1983)	Peel-Harvey (Backshall & Bridgewater 1981, Semeniuk & Semeniuk 1990.)	Leschenault (Pen 1992, 1993)	Walpole-Nornalup Inlet (unpublished data)	Princess Royal Harbour (Pen 1992)	Oyster Harbour (unpublished data)
Samphire marsh						
Sarcocornia quinqueflora	***	***	***		***	***
Wilsonia humilis			*		**	*
Hemichroa pentandra					***	*
Suaeda australis	***	**	***		**	**
Samolus repens	**		**		***	*
Triglochin striata	*		*		*	
Bolboschoenus caldwellii	**		*			
Halosarcia halocnemoides	***	***	***			*
Halosarcia indica bidens	***	**	***			
Halosarcia lepidosperma						***
Frankenia pauciflora	*(?)	*	***			
Gahnia trifida	(?)	*	*		*	*
Fringing vegetation or freshwater sedgeland						
Juncus kraussii	***	***	***	***	***	***
Baumea juncea	*		*		***	
Baumea spp sedgeland				*		
Isolepis nodosa			*		***	
Maireana oppositifolia						**
Atriplex hypoleuca					***	**
Calocephalus brownii					*	
Lepidosperma gladiatum					*	
Leptocarpus tenax				*		
Lepidosperma effusum				*		
Leucopogon obovatum				*		
Mangrove						
Avicennia marina			*			
Estuarine fringing forest / scrub						
Casuarina obesa	**	**	**			
Melaleuca cuticularis	*(?)	**	***	***	***	***
Melaleuca viminea	*(?)		*	*		
Melaleuca microphylla				*		
Freshwater fringing forest						
Eucalyptus rudis	***		***			
Melaleuca rhaphiopylla	***	**	***	***		
Melaleuca preissiana	*			*		*
Agonis flexuosa			*	*	***	*** *Agonis*
parviceps				*		
Callistachys lanceolata				***		** *Euca-*
lyptus cornuta						*
Astartea fascicularis				**		
Banksia littoralis				*		
Eucalyptus patens				*		
Hakea linearis				**		
Homalospermum firmum				***		
Kunzea sulphurea				**		
Total score	17	10	20	20	16	16

Asterisks (***, **, *) indicate relative importance to the characterisation of the fringing plant assemblages; (?) indicates difficult to assess due to clearing of vegetation and lack of clarity on old aerial photos.

The species assemblages along the shore of the Leschenault Inlet estuary are not more diverse than in other estuaries in south-western Australia. The species in this area are relatively common in other estuaries, and most of the assemblages find expression elsewhere albeit in reduced or restricted settings. What is important in Leschenault Inlet is the complex array of estuarine coastal habitats, and the salinity gradients developed therein have resulted in the development of a range of vegetation units that are distributed in mosaics and gradients across the various habitat types of the shoreline. Thus, the variation in assemblages across the three stages of development of bar-and-lagoon systems, or across the low bar and associated shallow shore-parallel lagoons on the high-tidal platforms represent distinct and important landscape ecological associations. This feature is important given that the stages of habitat development are dynamic *i.e.* they are on-going, and represent active habitat-evolving ecologic systems.

The complexities of the inter-relationship of vegetation to local and regional gradients in coastal landforms, the internal groundwater dynamics, and the effect of a south to north variation in estuarine source water salinity have not been fully explored in this study. However, the shore of the Leschenault Inlet estuary has the potential to provide a valuable natural laboratory for integrated vegetation-ecological investigations unlike any other estuary in south-western Australia. In this context, Leschenault Inlet estuary represents a classic classroom for student studies and research in estuarine peripheral vegetation ecology.

Additionally, Leschenault Inlet represents a valuable geoheritage and biodiversity resource. This is from a perspective of conservation given the array of vegetation units across the range of peripheral habitats, and the coastal landforms relating to a south to north gradient in landforms, coastal processes, groundwater hydrodynamics, and the effects of a variable and complex sealevel history (unique amongst the south-western and southern estuaries to Leschenault Inlet).

As noted above, in comparison to the other estuaries in Western Australia, the shoreline habitats and vegetation comprising the periphery of the Leschenault Inlet estuary rank as the most significant along the south-western coast of the Swan Coastal Plain, and ranks with the Walpole-Nornalup Inlet system which itself is located in the richest botanical district in south-western Australia. The presence of associations with winter ephemeral herbs and grasses within the peripheral vegetation formations links the Leschenault Inlet estuary with associations otherwise common only in Victoria (Bridgewater 1982) and indicates the special nature of Leschenault Inlet along the Western Australian coast.

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The white mangrove *Avicennia marina* in the Leschenault Inlet area

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Abstract

The white mangrove *Avicennia marina* (Forsk) Vierh forms local stands along the shores of Leschenault Inlet in three settings located in two main salinity regimes: the upper estuary where salinities vary from brackish water to hypersaline, and in the mainly marine Preston River Delta complex. At smaller scales, in the upper estuary *Avicennia* inhabits high tidal platforms, or front a steep dune shore where there is fresh water seepage. *Avicennia* is most common, however, in the Preston River Delta where there is daily marine tidal exchange. The three locations illustrate three different relationships between the occurrence and vegetation structure of *Avicennia* with respect to geomorphology and salinity. Within a given habitat, *Avicennia* occurs as scrub, heath, shrubland, and open shrubland and open heathland. Physiognomically, it forms single columnar-trunked shrubs, < 1 m high, varying to 3-4 m high, or multi-stemmed radially-branched shrubs 2-4 m high. Population structures of *Avicennia* cumulatively for the whole estuary show physionomic polymodality, and in various locations within its three main habitats there are adult-dominated populations different from seedling/sapling dominated populations. There have been changes in mangrove distribution and density over 60 years. The main changes are an increase of mangroves in the Preston River Delta, an increase in the extent of mangrove in front of the steep dune shore, and the establishment of small shrubs/saplings on high tidal platforms. *Avicennia* in Leschenault Inlet is scientifically important in that it represents the most southerly occurrence of this mangrove species in Western Australia. Five hypotheses are presented to explain this occurrence, ranging from a once widespread coastal distribution and then contraction to Leschenault Inlet during the latter Holocene, to *Avicennia* being only a recent late Holocene arrival to Leschenault Inlet. Preliminary analyses of pollen, and regional considerations suggest that *Avicennia* was not present along the south-west coast nor in Leschenault Inlet earlier in the Holocene. Later in the Holocene as more arid climates in Western Australia shifted northwards from Shark Bay to Exmouth Gulf and the shallow North West Shelf, the Leeuwin Current intensified, and *Avicennia* was established at Leschenault Inlet by delivery of propagules from northern populations. Its arrival in Leschenault Inlet may be a relatively recent event.

Keywords: mangrove, Avicennia marina, Leschenault Inlet, estuary, south-western Australia.

Introduction

As part of the collected papers on the estuarine environment of Leschenault Inlet, this paper describes local assemblages of the white mangrove *Avicennia marina* (Forsk) Vierh which forms local stands along the shores there. Despite being common and widespread in tropical Western Australia, the occurrence of *Avicennia marina* in this region constitutes a special situation in that it represents not only the most southern occurrence of the species in Western Australia but a disparate population with the next population some 500 km to the north.

While *Avicennia marina* in the Leschenault Inlet area has been noted in previous studies, reports, and surveys, no published study systematically describes its habitats and features of the vegetation. The first mention in the scientific literature of *Avicennia* in the Leschenault Inlet area was by Diels (1906) who noted the species (identified as *Avicennia officinales*) as part of a regional floral description, and also noted that it represented the most southern occurrence of the mangrove in Western Australia. Thereafter, mangroves in the Leschenault Inlet area have been noted in a variety of scientific publications (Sauer 1965; Smith 1985; Saenger *et al.* 1977; Semeniuk *et al.* 1978; Bridgewater 1982, 1985; Duke 1990 a,b, 1991).

Mangroves in Western Australia more typically occur in tropical environments as exemplified by the Pilbara Coast or Kimberley Coast, where there are mesotidal to macrotidal environments creating a complex array of habitats that support a variety of species (Semeniuk 1993a, b, 1996). The Leschenault Inlet area contrasts with these tropical settings in that it is located in a microtidal estuarine setting in a Mediterranean climate, extending the range of settings in Western Australia within which the species occurs.

The objective of this paper is to describe *Avicennia marina* in the Leschenault Inlet. The emphasis of the paper is on the description of the habitat setting of the mangrove, the structure and physiognomy of the mangrove, an inventory of the associated flora, and a description of the changes to the mangroves over the past six decades.

Methods

A variety of techniques were used to document the mangroves of Leschenault Inlet: examination of aerial photographs, establishment of transects through selected mangrove stands to document their relationship to habitats, site-based vegetation description, and laboratory analyses of soils, groundwater and soilwater.

Aerial photographs taken between 1941 and 1996 were used to define local geomorphic setting, determine the range of mangrove habitats available, and map the mangrove distribution in time. Transects through the mangrove populations were established to describe stratigraphy, depth to groundwater, soil types, and vegetation (Fig 2A), following Semeniuk & Wurm (1987). Transects were surveyed with

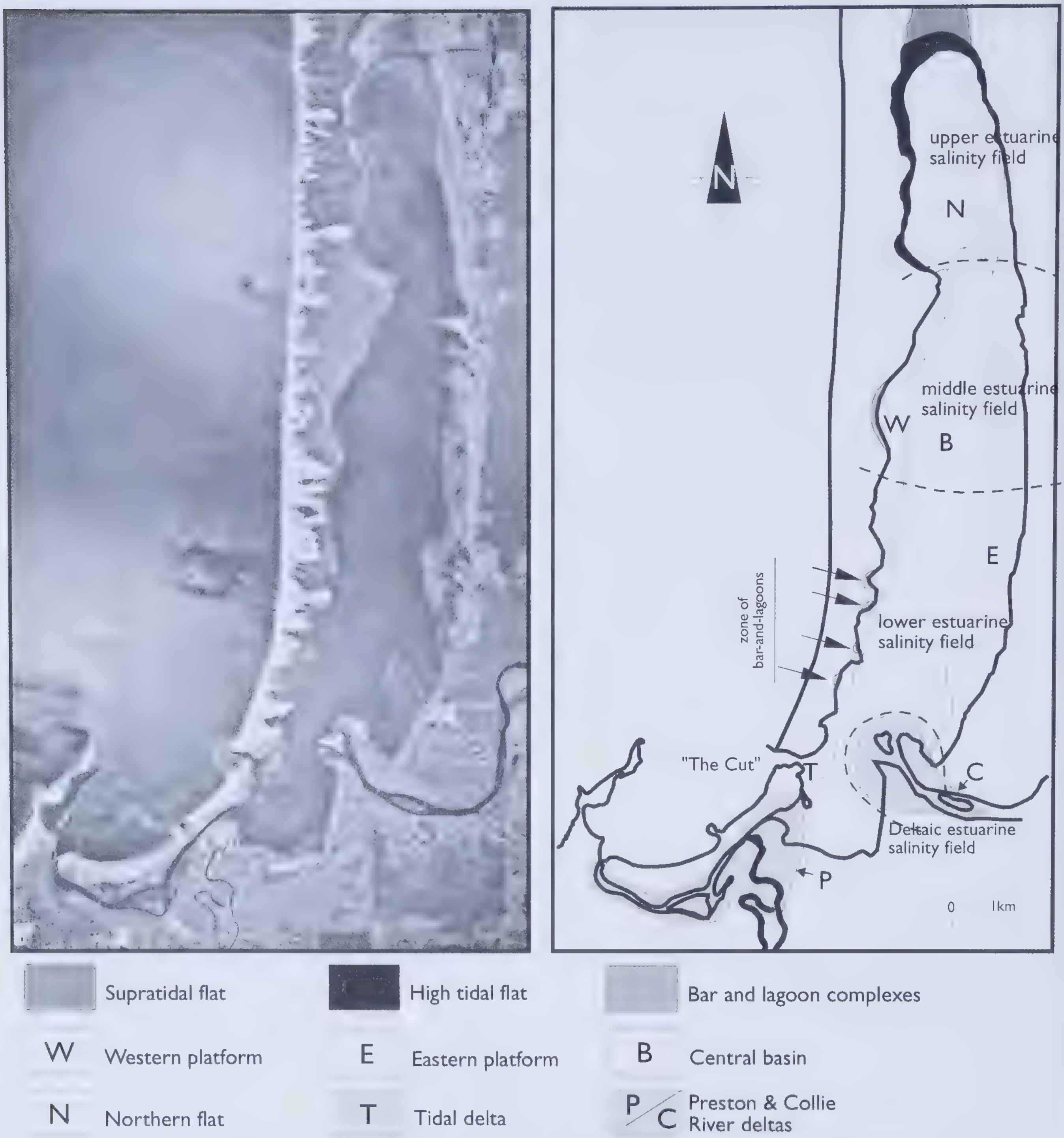


Figure 1. Aerial photograph (1966) of Leschenault Inlet showing nature of the elongate north-south oriented estuarine lagoon, and the deltaic complexes to the south prior to the anthropogenic impacts and map showing the distribution of estuarine units and salinity fields in Leschenault Inlet.

a dumpy level. Stratigraphy was determined by drilling and augering. Sediments in the stratigraphic sequence were described as to colour, fabric, texture and composition, and categorised to the main sediment groups of sand, muddy sand, sandy mud, and mud, and their shell-bearing equivalents. Piezometers were established at selected sites along transects to measure depth to water table and to sample water. Surface sediments for soil water determinations were collected at these selected sites, and frozen for transport and storage. Soil samples later were thawed and soil water salinity was determined following Semeniuk (1983). Salinity of groundwater samples and soil water samples were determined with a Cyberscan 200 TDS/Conductivity meter. Selected water samples were analysed for cationic content with an Atomic Absorption Spectrophotometer. Soil samples were wet sieved through standard Endecott Sieves at 1 ϕ intervals (Pettijohn 1957).

Vegetation structure, floristics, physiognomy, and the number of *Avicennia marina* individuals were documented and counted in replicate 5 m x 5 m quadrats along the

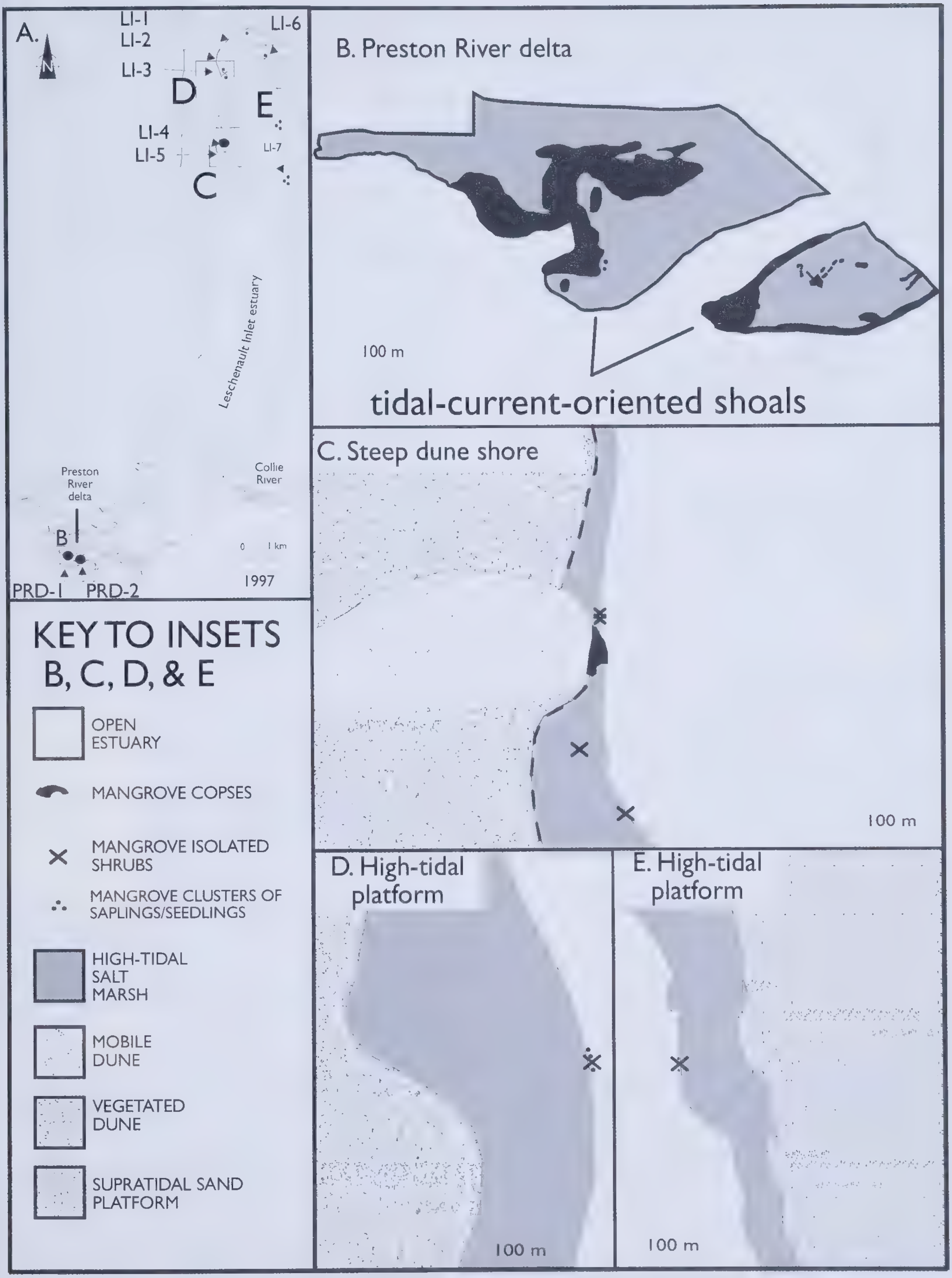


Figure 2. A: Location of study areas and transects. **B:** Map of mangrove occurrence in the Preston River delta, with mangroves mainly fringing the shoals. **C:** Map of occurrence of mangrove at the steep dune shore (advancing parabolic dune tip). **D & E:** Mangrove occurrence on the high tidal platforms.

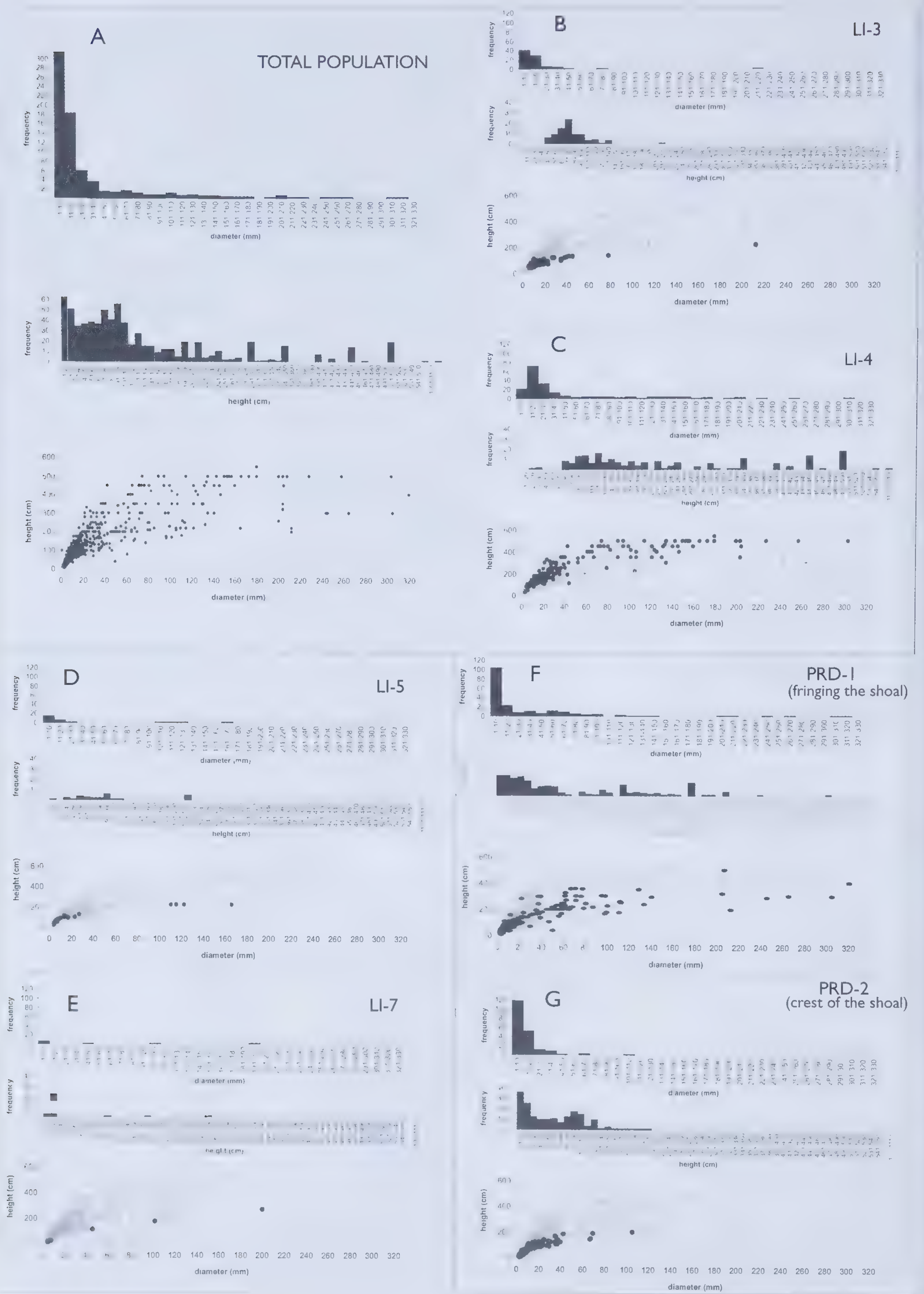


Figure 3. Population structures of *Avicennia marina*: legend continued over page.

Figure 3(continued): Graphs showing population structures of *Avicennia marina*. **A:** Total cumulative graphs for the whole of the Leschenault Inlet region. **B:** Graphs for Transect LI-3 (tidal flat platform). **C:** Graphs for Transect LI-4 (steep dune shore). **D:** Graphs for Transect LI-5 (high tidal platform). **E:** Graphs for Transect LI-7 (high tidal platform). **F:** Graphs for Transect PRD-1 (old stands fringing the tidal shoal crest of the Preston River delta). **G:** Graphs for Transect PRD-2 (recently recruited stands colonising the crest of a tidal shoal crest of the Preston River delta). While the data have been presented as plots for a given transect, specifically for the graphs of height *vs* diameter, the data for a given transect are presented against a background of the total cumulative graph of height *vs* diameter to illustrate seedling- or sapling-dominated patters, or adult-dominated patterns, or patterns of continuous recruitment against the total mangrove pattern.

Table 1. Terminology for and description of types of physiognomy of the mangrove plants at Leschenault Inlet estuary

Physiognomic term	Description of plant
seedling	generally single-stemmed plant up to 10 mm diameter and 30-40 cm high
sapling	generally single-stemmed plant up to 30 mm diameter, generally 30 or 40 cm high, up to 1 m high
young plant or shrub	single-stemmed plant up to 50 mm diameter, generally 1-2 m high
single columnar-trunked shrub	single-stemmed plant, generally 50-100 mm diameter, *ca* 1m high, varying to 3-4 m high
multi-stemmed erect- shrubs	generally 50-100 mm diameter, *ca* 1 m high, varying to 3-4 m high, locally 5 m high
multi-stemmed radially-branched shrubs	generally 50-100 mm diameter, *ca* 1 m high, varying to 3-4 m high, locally 5 m high
gnarled, recumbent, multi-stemmed radially-branched shrubs	generally 50-100 mm diameter, up to 300 mm diameter, 3-4 m high, up to 5 m high

transects. At a number of locations, representing the various habitat settings and physiognomic/structural types, *Avicennia marina* individuals were measured as to their height and trunk and stem diameter to describe the population in terms of size of mature plants, saplings and seedlings. Terminology for mangrove physiognomy is presented in Table 1 (and illustrated in Fig 7 of Semeniuk *et al.* 1978). Height was determined by a stadia marked in decimeters. Since measurement of stem and trunk diameters involved seedlings, saplings, young shrubs, and recumbent mature trees, measurement of DBH (diameter at breast height) was not possible. Trunk and stem diameters were measured at 10-20 cm from the ground. Measurements were obtained with a vernier calipers from two hundred plants from each selected locality.

Leschenault Inlet

Regional Setting

Leschenault Inlet is largely a shallow estuarine lagoon located along the coast within the southern part of the Swan Coastal Plain (Semeniuk & Meagher 1981), and in the Leschenault-Preston Sector of Searle & Semeniuk (1985). The estuarine lagoon is separated from the Indian Ocean by a barrier dune system, the Leschenault Peninsula (Semeniuk 1985a). The Leschenault Inlet estuarine lagoon is unique regionally in that it is the only estuarine system fronting the Rottnest Shelf that has been formed by a shore-parallel barrier dune complex, and that is wholly Holocene in age (Semeniuk 1985a).

Leschenault Inlet is set in a subtropical subhumid climate, or Mediterranean climate (Gentilli 1972), with an annual rainfall of 881 mm, an annual evaporation of 1984 mm. Tides are microtidal, usually diurnal, with a prevailing range of 0.5 m and a maximum range of 0.9 m.

From east to west, the three main landform and estuarine units bordering and constituting the Leschenault Inlet system are:

1. a high ridge of Pleistocene quartz sand and limestone, referred to the Mandurah-Eaton Ridge (Semeniuk 1997), and lowlands underlain by Pleistocene limestone referred to as the Yalgorup Plain (Semeniuk 1995a), both of which comprise the eastern hinterland;
2. Leschenault Inlet itself, which is an elongate shore parallel, shallow estuarine lagoon; and
3. a high quartz and carbonate sand dune barrier, the Leschenault Peninsula (Semeniuk & Meagher 1981), Holocene in age, that defines the western shore of the Leschenault Inlet.

The form of Leschenault Inlet, its internal features, and its shore types have been determined by several factors: the ancestral topography of the eastern hinterland (the Mandurah-Eaton Ridge and the Yalgorup Plain); the effects of a mid-Holocene higher sea level reworking the quartz sand of the Mandurah-Eaton Ridge; the orientation and extent of the Leschenault Peninsula; the eastward migration of parabolic dunes encroaching into the western margin of the estuarine lagoon from the Leschenault Peninsula barrier dune complex; and deltaic land buildups at the mouths of the Collie and Preston Rivers (Fig 1).

Prior to the 1950s, the Collie and the Preston River drained into the estuarine lagoonal environment. The Collie River formed a small wave-dominated delta (the Collie River Delta) to the south-east of the Leschenault Inlet, and the Preston River formed a tide-dominated delta (the Preston River Delta) in the southern part. The oceanic connection to the estuarine lagoon was via the river mouth of the Preston River (Semeniuk 2000).

A series of engineering activities from 1951 onwards has changed the nature of the estuarine lagoon and the river deltas:

- to facilitate exchange between the ocean and the estuary, a channel (known as "The Cut") was excavated through the southern part of the barrier dune opposite the Collie Delta, altering the hydrochemistry of the estuarine lagoon from one alternating from freshwater to saline to one dominated by marine conditions;

- much of the delta-land of the Preston River was infilled, thus severing the main body of the estuarine lagoon from the original oceanic exchange channel;
- the Preston River was diverted through a drain into the southern part of Leschenault Inlet; and
- the southern part of the Collie Delta was filled and drained for urban development.

Apart from local dredging for boat channels, and a rock-fill for a pipeline trestle, the nature of the internal geomorphology of the estuarine lagoon, however, has remained unchanged.

The central portion of the present Leschenault Inlet estuarine lagoon is a linear, shore-parallel, relatively deep mud-floored basin (generally 1.5-2 m deep). The eastern part of the lagoon where it adjoins the hinterland shore is a straight, shore-parallel, narrow, shallow water sand platform (tidal to about 1.0 m deep). The western part of the lagoon where it adjoins the barrier dune, has a multiple lobed shore as a result of the encroachment of parabolic dunes into the lagoon; the advancing front of the dunes has formed shallow water subtidal sand and muddy sand platforms and ramps (tidal to 1.5 m deep), and the interdune shores are protected small embayments underlain by mud and muddy sand.

Both east and west shores of the estuarine lagoon are mainly saltmarsh-vegetated high tidal platforms, the width varying from narrow (5-10 m) to wide (>500 m) depending on location in relation to mobile dunes, ancestral sand ridges, and erosional or depositional processes (Semeniuk 2000). The remnant of the Preston River Delta remaining after the construction of the harbour at Koombana Bay is a complex of linear, tidal-current-aligned shoals and emergent islands, with intervening shallow channels. The emergent islands are vegetated by samphires, rushes, or mangroves in the tidal zone, and terrestrial vegetation in supratidal parts.

There is a range of shore types developed along the periphery of the estuarine lagoon; these include (after Pen *et al.* 2000); 1) high tidal platforms vegetated dominantly by samphire or rushes; 2) tidal embayments (residing between dune corridors); 3) cliffed sandy shores where coastal erosion is incising into dunes; 4) steep dune shores where dunes are encroaching into the estuary; 5) bar and lagoon shores; 6) spits; 7) the Collie deltaic complex; and 8) the Preston deltaic complex.

There are three shore types that host mangroves (Fig 2): high tidal platforms; steep dune shores; and Preston River delta.

In terms of salinity structure, Wurm & Semeniuk (2000) subdivide the estuary into four zones, based on its variability over the seasons (Fig 1C): 1) an upper estuarine salinity field, where mean salinities approximate marine water, but show large variation in salinity, with brackish water common in the winter, and with hypersaline water in summer; 2) a middle estuarine salinity field, with mean salinities approximating marine water, but with moderate variation in salinity; 3) a lower estuarine salinity field, close to the marine source, where the salinities approximate marine water, with little variation; and 4) a deltaic zone, where the salinities approximate marine water, but exhibit marked freshwater patterns during flooding of the rivers.

There is a gradient of increasing groundwater salinity across the tidal flats, from marine at the water's edge to hypersaline towards the land. The hypersalinity is diluted by interaction with freshwater on a broad front from the barrier dunes, and is markedly diluted by freshwater seepage points from specific encroaching dunes (see below). The three main hydrologic sources and mechanisms pertinent to this study that maintain the mangroves are tidal recharge, freshwater seepage from dunes (Cresswell 2000), and meteoric recharge.

For tidal flat sites distant from freshwater seepage sites, the groundwater recharge mechanisms are tidal flooding and rainfall. During high tides and higher-than-normal prevailing winter water levels, estuarine water, largely of marine salinity, invades tidal flats and recharges the underlying groundwater. For sites proximal to barrier dunes, groundwater recharge is through tidal flooding, freshwater seepage, and rainfall. In regard to freshwater seepage, in winter, rainwater recharges groundwater under the dune barrier, and the water table rises forming locally steep hydraulic gradients along the shore (Cresswell 2000); these are the sites of freshwater seepage which reduce tidal flat salinities.

Avicennia marina in the Leschenault Inlet area

Some information on the biology and phenology of *Avicennia marina* in Leschenault Inlet area is in Semeniuk *et al.* (1978) and Duke (1990a, b, 1991). Duke (1991), using morphological characteristics and allozyme patterns, separated *Avicennia marina* into three groups (*viz A. marina* var *marina*, along the south-western and southern coast, *A. marina* var *australasica*, along the north-western to south-western coast, and *A. marina* var *eucalyptifolia*, along the northern and north-eastern coast). While Semeniuk *et al.* (1978) referred the species at Leschenault Inlet to *Avicennia marina* var *australasica* (Walp) Moldenke, later authors referred it to *Avicennia marina* var *marina* Moldenke (*cf* Tomlinson 1986; Duke 1991).

From a large scale habitat perspective, *Avicennia* occurs in Leschenault Inlet in two main salinity regimes: the upper estuary where salinities are variable from brackish water to hypersaline, and in the Preston River Delta complex. At smaller scales, in the upper estuary, mangroves inhabit high tidal platforms, or front a steep dune shore. The mangroves are best developed in the Preston River Delta setting, next in the steep dune shore setting, and least developed on high tidal platforms.

Within a given habitat, *Avicennia* occurs as scrub, heath, shrubland, and open shrubland and open heathland. Physiognomically, the mangrove forms single columnar-trunked shrubs, < 1m high, varying to 3-4 m high, or multi-stemmed radially-branched shrubs 2-4 m high. The population structures of *Avicennia* cumulatively for the whole of the Study Area, and in various locations within its three main habitats are shown in Fig 3.

To illustrate different aspects of population structure, data are presented in three ways: as stem diameters *vs* frequency, as plant height *vs* frequency, and as stem diameter *vs* plant height. The graph of diameter *vs* height illustrates, through occurrence of clusters of points and point outliers, the occurrence of recruitment phases in the populations. The graph of frequency of diameter classes next best illustrates population structure and recruitment phases.

The total cumulative data presented in Fig 3 illustrates the overall population structure of the Leschenault Inlet mangroves. The overall population structure for the whole of the study area shows a range of age classes, with a dominance of seedlings and saplings, grading to less abundant adults, reflecting the recent incursion of seedlings/saplings into the area. Population structures for the various populations in the three main habitats in the area are described below.

Apical extension and development of axillary shoots are a dominant form of canopy growth in the populations. There also is an abundance of lateral shoots (epicormic shoots) that develop and maintain branches in the adult plants. As the most southerly occurring outlier of *Avicennia marina* in Western Australia, phenologically there is variation in leaf growth and flowering and fruiting times compared to populations in tropical regions (Semeniuk *et al.* 1978). These observations are supported by the phenological studies of Duke (1990a) who compared phenology trends for Broome, Port Hedland, Carnarvon, and Bunbury as part of an Australia-wide survey. *Avicennia marina* in Leschenault Inlet generally commences flowering in March and April, with seed fall occurring in September (Semeniuk *et al.* 1978; Duke 1990a).

Avicennia in the Preston River delta complex

In the Preston River Delta area, *Avicennia* inhabits the tops and margins of tidally-aligned shoals and margins of emergent islands, respectively (Figs 4 & 5). These shoals and emergent islands are gently convex landforms, separated by shallow channels, and with upper surfaces located at *ca* mean sea level (MSL) to just above highest astronomical tide (HAT). Where bordered by narrow channels, the shoals or islands may be incised by the channel bank. Where bordered by broad channels, the edge of the shoal or island slopes moderately to subtidal. Landform, stratigraphy, substrate, groundwater and soil water salinity, and features of mangrove vegetation structure and density along Transect PRD-1 are presented in Fig 4. Salinity results of groundwater and soilwater in Transects PRD-1 and PRD-2 are presented in Table 2.

Stratigraphically, the shoals and islands consist of estuarine shelly sand capped by estuarine mud, sandy mud and muddy sand. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. This mangrove setting is distant from any freshwater seepage, consequently salinity gradients vary from marine to hypersaline from estuary to the crest of a shoal, and locally reverses to brackish water in the centre of emergent islands where elevation is sufficient to allow rainfall recharge. Groundwater salinity under the mangroves varies from 19 000 to 36 000 ppm, and soil water salinity varies from 31 000 to 72 000 ppm (Fig 4; and Table 2).

Table 2. Salinity of ground waters, surface waters, and soil waters along the various transects. Sites are noted on the transects in Fig 4. Shaded rows are soil water results; other rows are water results.

Site	Date	Surface water (ppm)	Ground water (ppm)	Soil water (ppm)
LI 1A	25/03/98		52 000	30 464
LI 1AB	25/03/98		53 000	30 036
LI 1B	25/03/98		55 000	40 878
LI 1BC	25/03/98		39 800	30 840
LI 1C	25/03/98		2 720	7 533
LI 2 Inlet	25/03/98		38 300	
LI 2A	25/03/98		53 200	38 155
LI 2AB	25/03/98			163 654
LI 2B	25/03/98		52 400	79 156
LI 2BC	25/03/98			46 182
LI2C	25/03/98		3 290	6 799
LI 3 Inlet	25/03/98	32 100		
LI 3A	25/03/98		47 000	36 511
LI 3AB	25/03/98			33 824
LI 3B	25/03/98		64 100	33 362
LI 3BC	25/03/98			65 008
LI 3C	25/03/98		3 380	10 971
LI 4 Inlet	25/03/98	32 800		
LI 4A	24/05/97		40 000	32 959
LI 4A	25/03/98			29 225
LI 4A/1*	25/03/98		27 400	
LI 4A/2*	25/03/98		40 100	
LI 4B	24/05/97		35 800	32 780
LI 4B	25/03/98			33 908
LI 4B/1*	25/03/98		30 800	
LI 4B/2*	25/03/98		37 900	
LI 4C	24/05/97		26 600	
LI 4C	25/03/98			31 872
LI 4C/1*	25/03/98		2 150	
LI 4C/2*	25/03/98		3 770	
LI 4 D	24/5/97		1 020	
LI 4 D	25/03/98			39 467
LI 4D/1*	25/03/98		820	
LI 4 D/2*	25/03/98		667	
LI 5 Inlet	25/03/98	35 300		
LI 5A	24/05/97		36 400	37 980
LI 5AB	24/05/97	37 000	44 000	48 978
LI 5A	25/03/98		63 200	30 877
LI 5B	24/05/97	31 300		29 450
LI 5B	25/03/98		52 100	37 198
LI 5C	24/05/97		374	
LI 5C	25/03/98		25 500	29 905
LI 6A	25/03/98		20 000	31 094
LI 6B	25/03/98		6 760	11 063
PRD 1A	25/03/98		36 500	31 373
PRD 1B	25/03/98		39 600	37 983
PRD 1C	25/03/98		17 000	72 261
PRD 1D	25/03/98		19 400	19 258
PRD 2 Channel	25/03/98	25 100		
PRD 2A	25/03/98		27 500	15 047
PRD 2B	25/03/98		32 800	28 342
PRD 2C	25/03/98		32 300	31 290
PRD 2D	25/03/98	26 600		
PRD 2D	25/03/98		32 300	27 832

1* = before bailing; 2* = after bailing

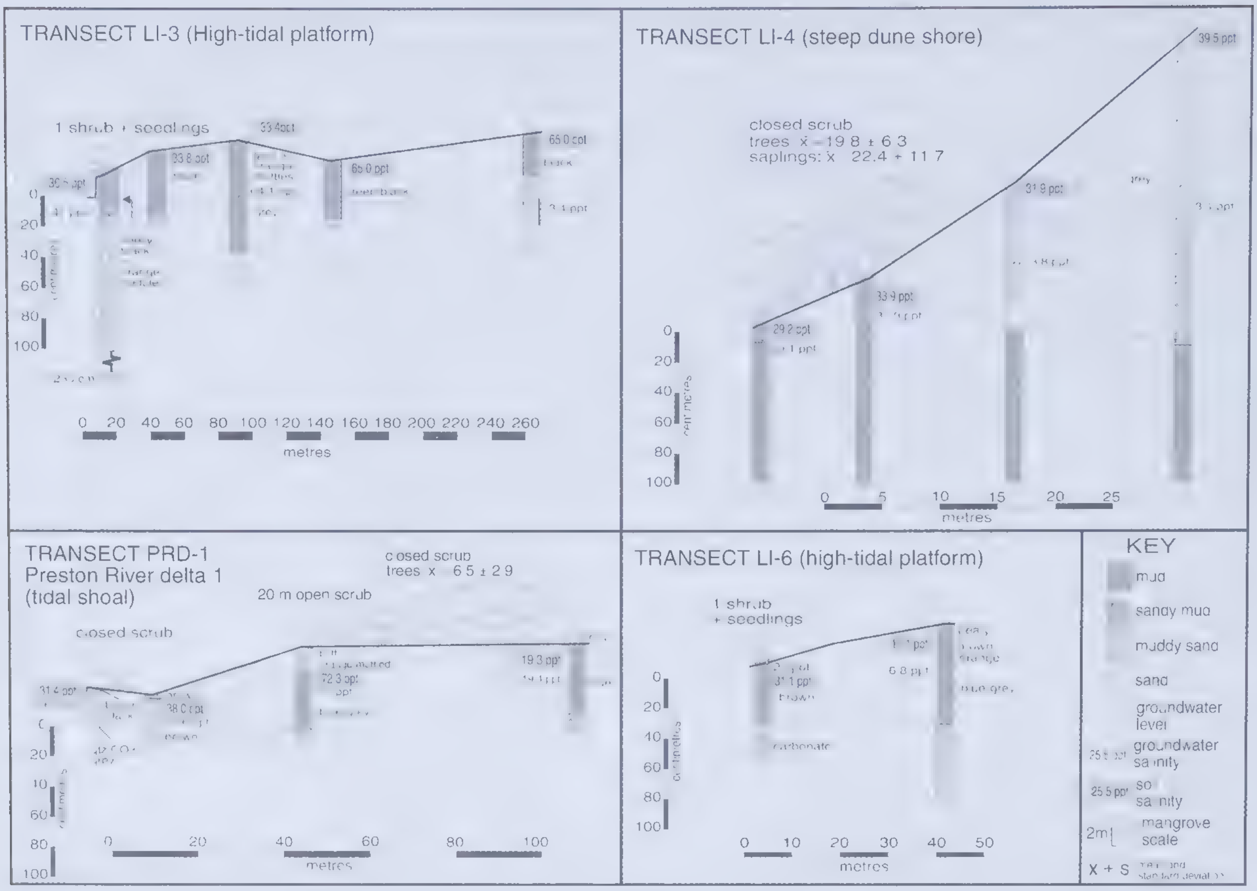


Figure 4. Profiles showing geomorphic and stratigraphic setting, groundwater and soil-water salinity, and information on the mangrove stands in terms of width of stand, height of stand, structure, and density.

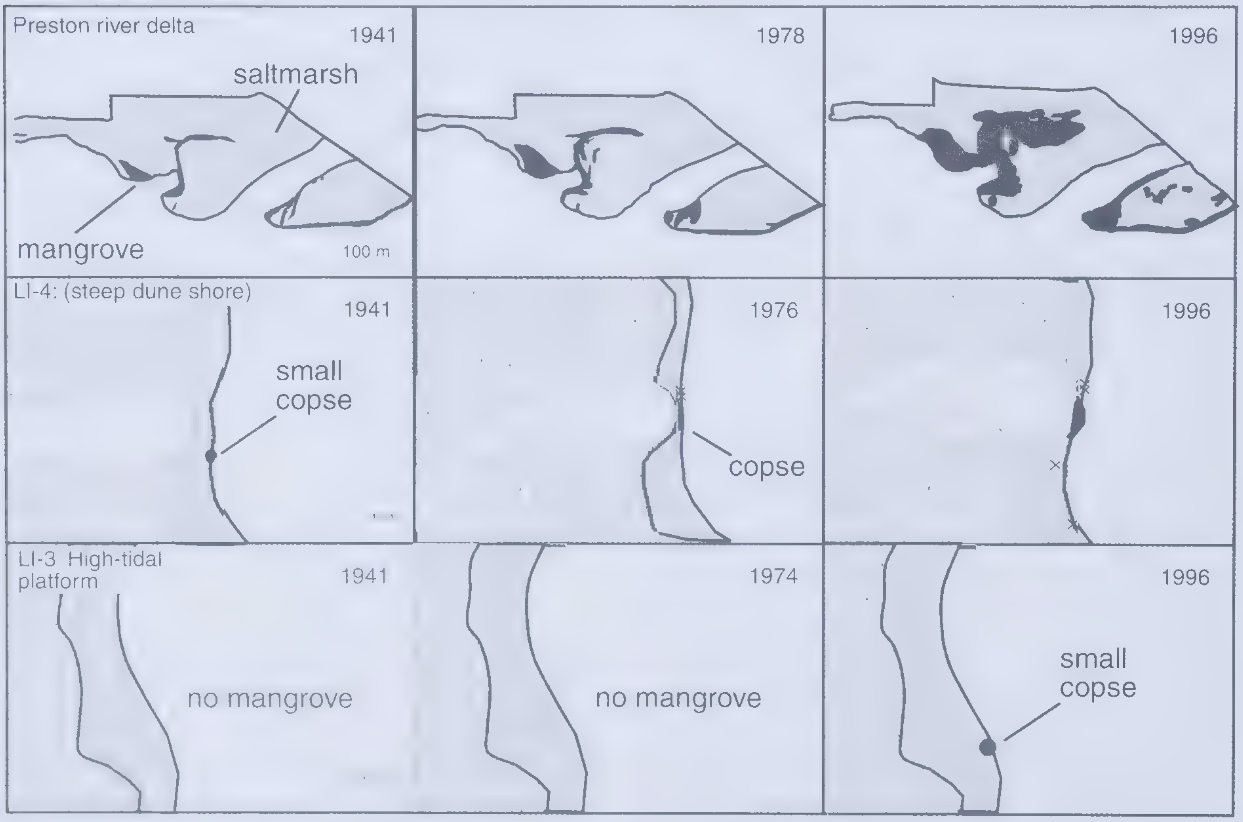


Figure 5. Changes in the extent of the mangrove in three habitat settings, *viz* the Preston River delta, the steep dune shore at Transect LI-4, and the tidal flat platform at Transect LI-3, based on aerial photography in 1941, 1974, 1976, 1978 (as indicated), and on ground-mapping and aerial photography in 1996.

Where inhabiting the margins of shoals or islands, *Avicennia* forms a narrow fringe several metres wide of multi-stemmed erect to recumbent-trunked scrub and single-stemmed erect to recumbent scrub, grading upslope to heath, with individuals mainly single-trunked, 4 m to < 1m high. If the margin of an island is erosionally cliffed, the tidal interval for mangrove may be removed, and terrestrial vegetation or riparian vegetation (*e.g. Casuarina obesa*) directly adjoins the deltaic channel. Where crests of shoals are at the appropriate tidal height, *Avicennia* forms scrub generally some 20 m wide, but up to 70 m wide. Where inhabiting the crests of shoals in association with a halophytic low heath of zoned *Sarcocornia quinqueflora* and *Halosarcia halocnemoides* subsp *halocnemoides, Avicennia* forms open heathland or isolated individuals, mainly single-trunked < 1 m to 2 m high, often lining small creeks. In the Preston River Delta area, there are two types of populations as described below.

In the past two decades, the populations of *Avicennia* have encroached over the tidal shoals and their margins of the delta complex through the dispersion of seedlings. The population structures of the mangrove of this area for three sites are shown in Fig 3. Along the margins of the shoals, where the mangrove populations have been extant since before the 1940s, the population now is comprised of seedlings, saplings, and mature adults, with a weak indication of phases of recruitment evident in the point outliers in the graph showing mangrove height *vs* diameter. Elsewhere along the margins of shoals, where the mangroves have encroached in the past two decades, the populations are dominated by seedlings, saplings, and some shrubs. On shoal crests, where there has been a widespread encroachment of mangrove in the past decade, the population is dominated by saplings and seedlings (Transect, Fig 3G). Thus in areas where the populations have been extant since at least the 1970s, adult plants dominate, but there is every gradation from seedlings to saplings to young plants and adults. In areas where the populations have encroached since the 1980s, seedlings and saplings dominate, and there is an absence of adults.

Avicennia adjoining steep dune shores

Avicennia inhabits a narrow tidal flat apron fringing a steep dune shore. The steep shore is the advancing front of a parabolic dune that is encroaching into the estuary. The tidal zone in front of the steep shore is a gently inclined surface, located between *ca* MSL and HAT, terminated along its estuary margin by a small cliff. A transect through this habitat showing stratigraphy, substrates, groundwater and soil-water salinity, and features of mangrove vegetation structure and density is presented in Transect LI-4 in Fig 4.

The stratigraphy under the dune and the tidal flat consists of estuarine mud, with a prism of dune sand that interfingers with and grades into the muddy sand and sandy mud of the tidal flat. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. This mangrove habitat adjoins a site of freshwater seepage, consequently, the salinity gradients vary from marine to hypersaline from estuary to land, and then reverse to brackish water at the site of the seepage. Groundwater salinity under the mangroves across the tidal flat varies from 37 000-40 000 ppm, with 3 400-3 800 ppm in the area of freshwater seepage, and soil water salinity varies from 26 000-35 800 ppm (Fig 4 and Table 2).

The mangroves form scrub and heath, some 15-20 m wide. Individual plants are small, single-trunk erect, to multi-stemmed erect, to locally, multi-trunked recumbent shrubs 4 m to < 1m high. While adult plants are dominant, there is a gradation from seedlings to saplings to young plants and adults.

In the past two decades, the population of *Avicennia* at this site has expanded. The population structure of the mangrove of this area is shown in Transect LI-4, Fig 3C. The mangroves here have been extant since before the 1940s, and the population is comprised of individuals from seedlings and saplings to mature adults, with no clear division recruitment phases. Essentially there has been continuous recruitment in the area for the past several decades.

Avicennia on high tidal platforms

Avicennia inhabits high tidal platforms that fringe the eastern and western shores of the estuary. These habitats are gently inclined to subhorizontal surfaces between *ca* MSL and HAT, commonly terminated along their estuary margin by a small cliff 10-30 cm high and bordered by mid-tidal to low-tidal sand flats and muddy sand flats. The surface of platforms locally may have shallow pools < 30 cm deep, or may be traversed by straight to meandering natural drainage channels generally 30-50 cm deep, locally up to 75 cm deep. Landward parts of the high tidal platforms are vegetated by *Juncus kraussii*, and more estuary-ward parts of the platform are vegetated by zoned *Sarcocornia quinqueflora, Halosarcia halocnemoides* subsp *bidens* and *Halosarcia halocnemoides* subsp *halocnemoides*. Transects through this habitat showing stratigraphy, substrates, groundwater and soil water salinity, and features of mangrove vegetation structure and density are shown in Transects LI-3 and LI-6 in Fig 4.

The stratigraphy underlying the high tidal platforms consists of estuarine sand or muddy sand, capped by root structured mud and sandy mud. Soils under the mangroves are bioturbated and root-structured muds and sandy muds. Since these mangrove habitats are distant from the dune shores and distant from any sites of freshwater seepage, groundwater recharge is through tidal flooding and rainfall. Groundwater and soil water salinity across the high tidal platform vary from 47 000-64 000 ppm and to 3 400 ppm in the zone of contact of the tidal flat with the barrier dunes, with 47 000 ppm in the area of mangrove habitation; soil water salinity varies from 33 000-65 000 ppm (Fig 4; Table 2).

The mangroves on the high tidal platforms tend to be very scattered to isolated, small, single-stemmed erect shrubs < 1 m to 2 m high, forming very open heathland emergent above a herbland. The vegetation associated with the mangrove is *Halosarcia halocnemoides* subsp *halocnemoides*, and *Sarcocornia quinqueflora*. Larger mangrove plants periodically flower, and often there is a mat of seedlings directly under the canopy in the pneumatophores of these plants, showing successful recruitment by seedlings from the overshading parent plant.

Aerial photographs from 1941, and observations from 1976 to 1987, indicate that *Avicennia* was generally absent in the high-tidal platform habitat in the northern part of the estuary, with only one occurrence along Transect 6 (extant since at least 1941). The populations of *Avicennia* along the high tidal platforms, however, have expanded since 1987. The population structure of the mangrove of this area is shown in Transects LI-3, LI-5 and LI-7 in Fig 3, and show the population dominated by saplings and seedlings, reflecting the recent incursion of mangroves into this area, and hence the youthfulness of the population.

Changes of mangroves through time

The aerial photographic record over six decades, and intermittent observations over 23 years indicate that there have been changes in the mangrove distribution and density in time (Figs 5 & 6). The main changes are the increase in abundance of mangroves in the Preston River Delta area, an increase in the extent of the population in front of the steep dune shore (Fig 5), the establishment of small shrubs and saplings on the tidal platforms, and the spread of mangroves in the northern part of the inlet.

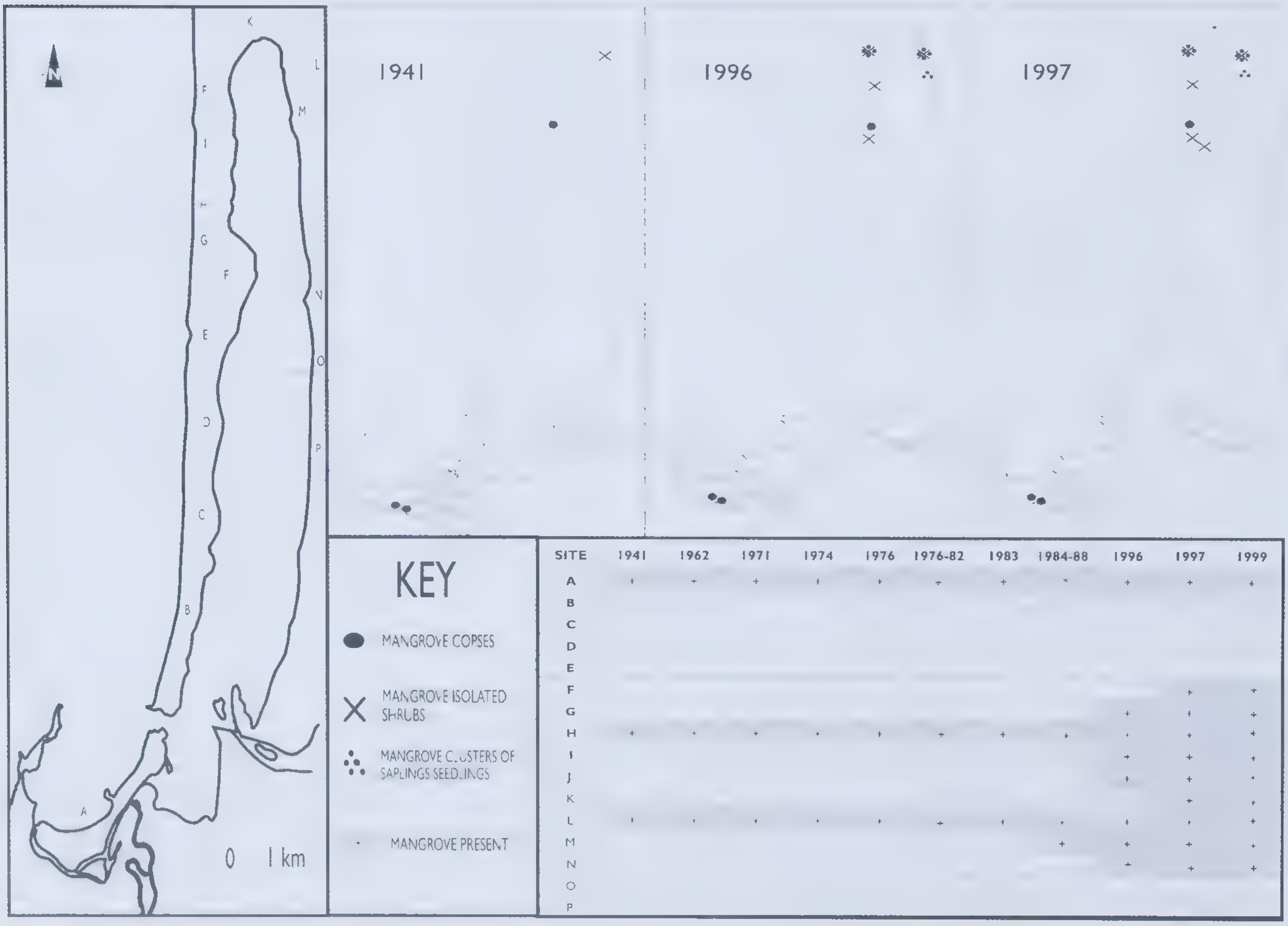
Discussion

Avicennia marina in Leschenault Inlet is discussed in terms of salinity fields as a major factor determining the occurrence and structure of the mangrove; the habitat approach, mangrove ecology, and anthropogenic impacts; the importance of freshwater seepage sites; the significance of the occurrences of *Avicennia* at Leschenault Inlet; hypotheses to explain the occurrence of *Avicennia* at Leschenault Inlet, evidence of the pollen record, and the biogeographic setting of the species.

Salinity fields and mangroves

The three settings of mangroves in the Leschenault Inlet area essentially illustrate three different relationships between the occurrence and vegetation structure of *Avicennia marina* with respect to salinity regimes:

1. Preston River Delta setting: a tidal flat with daily marine flooding; this is the normal and generally prevailing setting for *Avicennia* globally and elsewhere in Australia; as a result of the near-marine salinities, the mangrove forms well-developed scrub formations;



SITE	1941	1962	1971	1974	1976	1976-82	1983	1984-88	1996	1997	1999
A	+	+	+	+	+	+	+	+	+	+	+
B											
C											
D											
E											
F										+	+
G									+	+	+
H	+	+	+	+	+	+	+	+	+	+	+
I									+	+	+
J									+	+	+
K										+	+
L	+	+	+	+	+	+	+	+	+	+	+
M								+	+	+	+
N									+	+	+
O											
P											

Figure 6. Occurrence of the mangrove along various transects A-P, based on aerial photographic interpretation for the years 1941, 1962, and 1971, on aerial photographs and field observations for the years 1983 and 1996, and on field observations for the years 1976-1982, 1984-1988, 1997 and 1999.

2. steep dune shore setting: a hypersaline tidal flat with freshwater seepage to dilute the hypersalinity; this is a site of groundwater perturbation that allows mangroves to colonise saline environments (*cf* Semeniuk 1983); as a result of the near-marine salinities, again, the mangrove forms well-developed scrub formations; and
3. high tidal platform setting: a hypersaline tidal flat without freshwater seepage; as a result of the hypersalinity the mangrove occurs as scattered and isolated small individuals.

Habitats, ecology and anthropogenic impacts

This paper has documented the various formations of *Avicennia marina* within different habitat settings within Leschenault Inlet. It provides a baseline description of *Avicennia* in this region, and provides insight into the variety of edaphic, hydrologic, and hydrochemical environments that determine the occurrence of the species in an estuarine setting. In contrast to the richer variety of habitats that *Avicennia marina* colonises in tropical areas, Leschenault Inlet provides only a limited range, but nonetheless this can provide important information about mangrove ecology, in terms of the effects of stratigraphy, soils, tidal recharge *vs* freshwater seepage, hydrochemistry, hydroperiod, and nutrients, particularly since the species is at the geographic limit of its latitudinal occurrence in Western Australia. Where a species is at the limits of its natural geographic range, as *Avicennia* is in the Leschenault Inlet area, environmental determinants may be at threshold values for determining the species' response, and environmental effects thus may be amplified or exacerbated. For instance, the three habitat settings for *Avicennia* in the Leschenault Inlet area have different geomorphic, stratigraphic, hydroperiod, and hydrochemical features, and *Avicennia* has responded by developing populations with varied structural and physiognomic features. As such, these different habitat settings can function as valuable natural laboratories for research into the response of *Avicennia* to various physical, chemical and biological determinants of mangrove autecology.

For example, the anthropogenic alteration of Leschenault Inlet through harbour development and channel incision may have had a long-term effect on the mangrove populations. The slow expansion of *Avicennia* populations, and the slow general increase in height of the formations may be linked to the overall increased salinity of the estuary following the excavation of "The Cut", and the blocking through landfill of the Preston River Delta from its freshwater source so that now it is essentially a shoal-and island-clogged tidally flushed marine inlet. These engineering and hydrochemical changes, and the slow decadal-long response of *Avicennia* populations provide insight into determinants of *Avicennia* ecology in a regional context, but also underscore the problem that in situations where species are slow to respond to physico-chemical changes, that anthropogenic impacts may take decades to manifest.

Freshwater seepage sites

Maintenance of mangrove by daily tidal recharge is a well established process in tropical and temperate settings (Clarke & Hannon 1970; Chapman 1976; Tomlinson 1986), and the occurrence of mangroves in the Preston River Delta and on high tidal platforms conforms to this general pattern. Freshwater seepage also can be important in maintaining mangrove habitats, such as along upper tidal flats (particularly salt flats) in tropical environments (Semeniuk 1983). An important factor to emerge from this study is the association of mangroves with freshwater seepage, contrasting those maintained by tidal recharge (high tidal platforms and the Preston River Delta) from those partly maintained by freshwater seepage (steep dune shores). The importance of freshwater seepage thus is extended from tropical environments to Mediterranean climate settings.

The interaction between freshwater seepage and geomorphology to develop mangrove habitats in the Leschenault Inlet area, however, is subtle. While there is over 30 km of tidal flat circumferential to Leschenault Inlet, with development of wide high tidal platforms, there are only limited sites of freshwater seepage appropriately placed with potential to develop mangrove habitats. Along the western margin, for example, there is a general low level seepage of freshwater that results in kilometres of fringing *Juncus kraussii* rush between the dunes and the high tidal platform, the latter being colonised by herbaceous halophytes such as samphires. Also there are local more directed freshwater seepage sites manifest as perturbations in vegetation associations or as freshwater pools (Cresswell 2000). These general ubiquitous freshwater seepage interfaces and mosaics, however, are not inhabited by mangroves. Similarly, there are steep dune shores with freshwater seepage that abut the estuary margin, but the appropriate tidal level for potential mangrove growth is encompassed in a cliff.

Assessing the overall occurrence of fresh water seepage zones and mangroves in Leschenault Inlet leads to the conclusion that seepage zones, if they are to develop mangrove habitats, need to satisfy the following criteria:

- the freshwater seepage must be able to penetrate into the mid to upper tidal zone, where mangrove can colonise *i.e.* a steep hydraulic gradient in the freshwater system, or a distinct hydrologic pathway, or a linear incursion of a dune into the estuary that carries with it a finger of freshwater; and
- that there is no cliff along the estuary shore at the level where mangroves may be developed (usually, steep sandy shores are the most prone to wave attack, and hence develop cliff lines).

A summary of the various tidal environments in Leschenault Inlet, their relationship to freshwater seepage, and the reasons for the presence or absence of mangrove is presented below in Table 3.

In this context, it can be seen that the occurrence of *Avicennia* along the estuarine shore in zones of marked freshwater seepage is the result of distinct combination of geomorphic and hydrologic situations.

Significance of *Avicennia* at Leschenault Inlet

Avicennia marina in the Leschenault Inlet area, at latitude 33° 17' S, does not constitute the most southern occurrence of the species in the southern hemisphere globally. *Avicennia marina* occurs at higher latitudes in Victoria (Bridgewater 1982) at Corner Inlet (latitude 38° 45' S) and Western Port Bay (latitude 38° 22' S), and in South Australia, formerly as far south as Port Lincoln (latitude 34° 45' S), and is still extant as far south as Tumby Bay (latitude 34° 20' S). However, *Avicennia* in Leschenault Inlet is scientifically important in that it is the most southerly occurrence of this species in Western Australia, and as such it can provide valuable insights into climatic history and the dynamics of the Leeuwin Current. The nearest other coastal occurrence in Western Australia is along the coastal sector between Shark Bay and Carnarvon (latitude 24° 53' S), and the general nearest occurrence is offshore from the mainland at the Houtman Abrolhos Islands (latitude 28° 40' S). As will be discussed later, the mangrove stands at Leschenault Inlet, Houtman Abrolhos Islands, and Carnarvon may be inter-related.

Occurrence of *Avicennia* at Leschenault Inlet

Avicennia marina in the Leschenault Inlet area forms a very isolated occurrence in Western Australia. The nearest other locations of this species are the Houtman Abrolhos offshore from Geraldton, and Shark Bay on the mainland coast, essentially 500 km and 1 000 km distance, respectively. From a broader perspective, there are several critical regional maintenance factors that relate to the occurrence and survival of *Avicennia* in any given area (MacNae 1968; Walsh 1974; Chapman 1976; Oliver 1982; Tomlinson 1986; Hutchings & Saenger 1987): appropriate habitats, in terms of substrate, salinity, and low wave and tidal energy; adequate means of reproducing, either vegetatively or sexually; external seed source, if the population is not maintaining itself internally; adequately warm sea temperatures; adequately warm air temperatures; and no frost.

Table 3. Relationship between tidal environments, freshwater seepage and mangrove occurrence.

Setting	Description	Mangrove occurrence
dune abutting wide high tidal platform; freshwater seepage along the contact	Juncus kraussii developed along dune and high tidal flat interface	no mangroves - freshwater seepage developed above HAT
narrow, cliffed, high tidal platform; weak freshwater seepage from the upper slope	Juncus kraussii locally developed along HAT zone, no other vegetation developed	no mangroves - interval of potential mangrove occurrence encompassed in a cliff
steep dune margin cliffed at shore, with freshwater seepage from dune to estuary	sand cliff fronted by low tidal sand flat	no mangroves - interval of potential mangrove occurrence encompassed in a cliff
steep dune margin, with dune incursion into the estuary, and strong freshwater seepage into tidal zone	Avicennia marina developed in front of dune	mangrove present - appropriate tidal level developed, with freshwater seepage

Expression of these factors in the Leschenault Inlet area are listed in Table 4 below (data from Anon 1975; Pearce & Walker 1991; and this paper).

The other main estuaries along the coast between Shark Bay and Leschenault Inlet, termed here the Southwest-Coast Estuaries (including the estuaries of the Murchison, the Hill, the Moore, the Swan-Canning Rivers, and the Peel-Harvey system), though they have appropriate low energy tidal habitats and salinity, do not support *Avicennia marina* populations. These other estuaries, however, support halophytes such as *Haloscarcia* spp, *Suaeda australis*, and *Sarcocornia* assemblages (Cresswell & Bridgewater 1998) which colonise habitats (in terms of substrates, wave and tidal energy processes, and salinity) similar to mangrove habitats in Leschenault Inlet, and which cohabit with *Avicennia marina* in the Leschenault Inlet area. This implies that there are appropriate habitats for *Avicennia* in these other estuaries, yet there is a large gap along the coast with the mangrove absent between Leschenault Inlet and Shark Bay on the mainland, and the Houtman Abrolhos its nearest mangrove neighbour latitudinally. However, it should be

Table 4. Factors determining occurrence of Avicennia in Leschenault Inlet.

Maintenance factor	Expression in Leschenault Inlet
appropriate habitats	abundant in Leschenault Inlet
adequate means of reproducing	mangroves in Leschenault Inlet reproduce and maintain their populations both sexually and asexually
external seed source if population is not maintaining itself internally	potentially from northern waters via the Leeuwin Current
warm sea temperatures	derived from the Leeuwin Current
warm air temperatures	subtropical air temperatures; mean maximum summer temperature is 27.9 °C, mean minimum winter temperature is 8.3 °C
frost	frost is generally absent in the region of Leschenault Inlet

noted that other halophytic species are actually broadly distributed within the saline interior of the south-west region, and their origin today on south-coast estuaries could be related to the transport of seed by rivers. Such an avenue for distribution of plant species is not available to the mangrove.

We present and test five hypotheses to explain this distribution.

1. *Avicennia* was more widespread along the coast earlier in the Holocene with a more arid climate, but with a shift of aridity northwards over the late Holocene through Earth axis precession (Glassford 1980, Reichelt cited in Semeniuk 1995b), and the contraction of coastal populations to Shark Bay, mangroves at Leschenault Inlet are a relict outlier, surviving, but not linked to warm waters of the nearby Leeuwin Current.
2. *Avicennia* was more widespread along the coast earlier in the Holocene, as described above, but with a shift of more arid climates to the north over the late Holocene it remained at Leschenault, continuing to survive only because of the effects of the warm waters of the Leeuwin Current.
3. *Avicennia* was never present generally in estuaries, along the south-west coast earlier in the Holocene, and its occurrence at Leschenault Inlet initially was established by the delivery of propagules by the Leeuwin Current earlier in the Holocene when conditions were more arid; the population continues to be maintained by relatively warmer water where this Current impinges on the coast, in contrast to coastal areas immediately further north, and by the ongoing periodic delivery of propagules.
4. *Avicennia* was never present generally along the south-west coast earlier in the Holocene, and while the population at Leschenault Inlet initially was established by the delivery of propagules from the Leeuwin Current, the population continues to be maintained now by relatively warmer water where this Current impinges on the coast, and reproductively it is now internally self sustaining by adequate seedling production and survival without the need for periodic propagule delivery from the Leeuwin Current (this hypothesis is very similar to Hypothesis 3).
5. *Avicennia* was never present generally along the coast nor in Leschenault Inlet earlier in the Holocene, and as more arid climates in Western Australia shifted northwards from a centre on Shark Bay to Exmouth Gulf and the shallow North West Shelf (Semeniuk 1995b), the Leeuwin Current intensified, and the population at Leschenault Inlet was established by the delivery of propagules from northern populations late in the Holocene; as such, the arrival of the mangrove is a relatively recent event in the Holocene.

Hypothesis 1: *Avicennia marina* was once more widespread along the south-west coast, essentially occurring in all the southwest-coast estuaries between Shark Bay and Leschenault Inlet earlier in the Holocene, and since then, with a climate change, and a shift of the axis of aridity to further north in response to Earth-axis precession (Glassford 1980, Reichelt cited in Semeniuk 1995b), there was a concomitant shift and contraction of the species to the north. In this context, the occurrence of *Avicennia* at Leschenault Inlet would appear to represent a relict outlier population.

Evidence to partly support this hypothesis would be *Avicennia* pollen in Holocene sediment in other Southwest Estuaries. However, examination of appropriate Holocene sediments in the Swan-Canning River estuary, and the Peel-Harvey River estuary, the nearest neighbouring estuaries with similar tidal habitats, has not uncovered fossil *Avicennia* pollen. Absence of pollen as evidence for absence of the mangrove, however, is equivocal, because even if *Avicennia* was formerly present at these sites, long-term preservation of its pollen could depend on appropriate taphonomy and absence of bioturbation and reworking.

Another line of evidence for this hypothesis comes from archaeological studies in Shark Bay where Stevens (1994) concluded that it was possible that *Avicennia* populations were more widespread earlier in the Holocene, and that they had contracted in response to increasing basin water salinity (*cf* Hagan & Logan 1974), and in response to a possible Holocene climate change as the axis of aridity shifted northwards. From this perspective, the contraction of *Avicennia* populations in the Shark Bay area would represent a small scale pattern of a subcontinental-scale phenomenon *i.e.* the elimination of *Avicennia* from the Southwest Estuaries, and their contraction to the north. If this hypothesis is correct, then it would remain to explain why *Avicennia* remained as a relict population in the Leschenault Inlet area only.

Hypothesis 2: This hypothesis is similar to that above, but with an explanation as to why *Avicennia* was not eliminated from Leschenault Inlet as the zone of aridity migrated northwards, whereas it was eliminated from the estuaries further north. Such an explanation rests on the premise that coastal zones proximal to Leschenault Inlet today are bathed in warmer water than coastal waters located further north between Leschenault Inlet and Moore River estuary. Thus, with the shift of the arid climate to the north, and the elimination of *Avicennia* from the Southwest Estuaries, the species remained as a relict outlier of its once more extensive distribution because the Leeuwin Current provides a local warm water quasi-tropical setting in the Leschenault Inlet area enabling the species to persist.

Hypothesis 3: *Avicennia marina* occurs in Leschenault Inlet and solely in this region along the south-western Australian coast because eddies of the warm water Leeuwin Current periodically impinge on the coast in the Geographe Bay area, with some of this warm water deflected northwards as eddies towards the coast at Bunbury and into the Leschenault Inlet. Thus, there is potential that *Avicennia* propagules earlier in the Holocene, and up to the present, had been and are carried from northern more tropical waters. Once established in Leschenault Inlet, the relatively slightly warmer waters of the coastal zone maintained the populations. The dispersal of *Avicennia* propagules, traversing the 500 km between Houtman Abrolhos and Leschenault Inlet, may have involved direct delivery from the Houtman Abrolhos to Leschenault Inlet involving weeks of transport, or may have involved island-hopping.

A velocity of 0.2 m s^{-1}, at times 0.5 m s^{-1}, for the Leeuwin

Current, as reported by Cresswell (1991), could readily deliver *Avicennia* propagules from Houtman Abrolhos to Leschenault Inlet in 3-4 weeks. Clarke (1993) found that *Avicennia marina* var *australasica* propagules in south-eastern Australia can have medium term viability, surviving enforced dispersion for up to 5 months. A similar propagule viability for *Avicennia marina* var *marina* in Western Australia would implicate the Leeuwin Current as a possible direct delivery mechanism. Propagules from the region of Houtman Abrolhos would be entrained in the current and periodically delivered to the Bunbury area.

Alternatively, the *Avicennia marina* may have migrated from Houtman Abrolhos to Leschenault Inlet by island hopping *i.e.* there were small temporary sexually reproducing populations of *Avicennia* established on the string of islands and reefs located offshore from the mainland in the Cape Bouvard to Trigg Island Sector and the Lancelin to Dongara Sector of the Rottnest Shelf Coast (Searle & Semeniuk 1985), and these delivered propagules in turn along the chain of islands and reefs. This model would allow for dispersion of the species from island to island within the time of short term viability of its propagules. Currently, the islands and reefs offshore from the Western Australian mainland between Houtman Abrolhos and Garden Island do not support *Avicennia* stands, but given that these islands and reefs would have been larger earlier in the Holocene, and that with continuing bioerosion and wave erosion of these structures (Semeniuk 1985b), they have diminished to the size they are today, it is plausible that they lost their mangrove habitats over the period of the middle to late Holocene.

If Hypothesis 3 is correct, it would mean that *Avicennia* was not formerly more widespread along the mainland coast, and that *Avicennia* at Leschenault Inlet is not simply a relict residual population from these earlier times. The evidence to support this hypothesis includes the fact that the Leeuwin Current is a warm water, relatively fast moving offshore but shore-parallel current deriving from the tropical regions, that it carries tropical zooplankton and larvae, that it impinges on the coast in the vicinity of Leschenault Inlet, and that the other occurrence of *Avicennia* south of Shark Bay is in the Houtman Abrolhos Islands, in the path of the same current. From this perspective, the occurrence of *Avicennia* populations in the Leschenault Inlet area would represent a region where the Leeuwin Current interacts with the coast.

However, if Hypothesis 3 is correct, then it would remain to explain why *Avicennia* is absent from the Vasse and Wonnerup estuaries, where the Leeuwin Current *directly* impinges on the coast, and where marine seagrasses and algae in Geographe Bay reflect these quasi-tropical oceanic conditions. Its absence may be explained from a consideration of the original natural hydrochemistry of the Vasse and Wonnerup estuaries. Formerly, in the natural situation, both the Vasse and Wonnerup estuaries were largely barred and freshwater systems, and the fringing vegetation was/is *Melaleuca rhaphiophylla, Melaleuca cuticularis* and *Juncus kraussii*, indicating the extent of freshwater influence within the estuary. To place the significance of these species in hydrochemical perspective, in Leschenault Inlet, *Melaleuca rhaphiophylla, Melaleuca cuticularis* and *Juncus kraussii* along the tidal flat and dune margins indicate marked to very marked freshwater seepage to the extent that groundwaters approximate freshwater wetland systems. These freshwater-dominated habitats do not support *Avicennia* even though the species is present in the estuary. The species is best developed in the Preston River Delta complex (where there is daily exchange with marine water), and in the upper estuary where source waters became hypersaline and there is freshwater seepage to dilute this hypersalinity but insufficient to create a freshwater-dominated system.

Hypothesis 4: This is similar to Hypothesis 3, in that the Leeuwin Current earlier in the Holocene, perhaps under more arid conditions, originally delivered propagules of *Avicennia marina* to Leschenault Inlet, but once the mangrove population established, they became self-sustaining through vegetative reproduction and seedling production. Studies of population dynamics, fruiting, and seedlings over the past two decades show that mangrove populations within Leschenault Inlet indeed are self-sustaining and expanding through internal recruitment.

Hypothesis 5: This proposes that *Avicennia* is a very recent (late Holocene) arrival in Leschenault Inlet, reflecting a possible intensification of the Leeuwin Current as the maximum zone of aridity encroached onto the shallow waters of the Northwest Shelf. The Leeuwin Current then delivered mangrove propagules from northern populations.

Elimination of Hypotheses 1, 2, 3 and 4, and support of Hypothesis 5 rests on the fossil record of mangrove pollen in Leschenault Inlet and in estuaries further north, as described below (Semeniuk *et al.* 2000).

Evidence from the pollen record

The preliminary studies of pollen from the sedimentary record of Leschenault Inlet indicate that *Avicennia marina* was not present in the region earlier in the Holocene. The study of fossil tidal flat estuarine sediments from Peel-Harvey estuary and the Swan River estuary show that *Avicennia marina* may not have been present there earlier in the Holocene. The patterns of occurrence of *Avicennia marina* pollen in relation to stratigraphy and age are summarised in Table 5. More details for the pollen occurring within Leschenault Inlet, in terms of sampling sites and its taphonomy are provided in Semeniuk *et al.* (2000).

Milne (University of Western Australia, Department of Geography, *pers. comm.*) and Waterhouse (University of Western Australia, Department of Geology and Geophysics, *pers. comm.*) examined the palynological slides prepared from sediments described above, scanning 1 500 pollen grains for each slide to determine whether *Avicennia* was present. These data suggest *Avicennia* was not widespread along the south-western estuaries, and that it was not even present earlier in the Holocene in Leschenault Inlet. Effectively, Hypotheses 1-4 are eliminated. The limited data do, to date, support the suggestion that *Avicennia* is a very recent late Holocene arrival in Leschenault Inlet. If this is correct, and if it is linked to the shift northwards of more arid climates due to precession of the Earth's axis, this would suggest a possible intensification of the Leeuwin Current, or an intensification of warm water contribution from the Northwest Shelf into the Leeuwin Current, as the maximum zone of aridity encroached onto the shallow waters of the Northwest Shelf. The Leeuwin Current then delivered mangrove propagules from northern populations. The warm water impinging on the coast in the Geographe Bay to Bunbury area sustains the *Avicennia* population in the Bunbury area in quasi-tropical marine conditions.

However, these results must be viewed as preliminary, and it is suggested that a more wide-spread survey of estuarine tidal flat sediments in the south-western estuaries be undertaken to more conclusively determine that *Avicennia* pollen is absent.

Biogeography

Several authors have attempted to assign the mangrove populations of Leschenault Inlet to a biogeographic setting (Saenger *et al.* 1977; Semeniuk *et al.* 1978; Bridgewater 1985; Bridgewater & Cresswell 1999). In considering the species richness of mangrove assemblages along the Western Australian coast, Saenger *et al.* (1977) designated three mangrove regions, and placed the *Avicennia* populations of Leschenault Inlet into their southern region 5W Region, linking it with *Avicennia* in the Carnarvon/Gascoyne region.

Based on climatic considerations and species richness of mangrove assemblages of Western Australia, Semeniuk *et al.* (1978), delineated four mangrove biogeographic zones. The Gascoyne Delta, Carnarvon and Shark Bay region were linked with the Bunbury region, and placed in Biogeographic Region IV, all having only *Avicennia marina*.

Bridgewater (1985), in considering halophytic understorey in association with *Avicennia*, proposed that the *Avicennia* populations in the Gascoyne region represented the extremity of a cline from the Pilbara region, and that it would be better associated with the mangroves of the Pilbara, and isolated the mangroves at Leschenault Inlet as a separate region.

Bridgewater & Cresswell (1999) place the Leschenault

Table 5. Region-wide results of sampling for *Avicennia* pollen in Holocene deposits.

Setting for pollen sample	Age (years BP)	*Avicennia* pollen	Implications
sediment under modern mangrove scrub, Leschenault Inlet See Semeniuk *et al.* (2000)	modern	yes	mangrove pollen preserved, thus useful to infer occurrence of *Avicennia*
sediment in other estuarine environments in Leschenault Inlet See Semeniuk *et al.* (2000)	modern	yes	mangrove pollen preserved, thus indicating that Avicennia pollen is adequately dispersed to implicate its presence
recent fossil sediment, under saltmarsh flats along north, eastern and western coasts of Leschenault Inlet where there is no occurrence of mangrove today See Semeniuk *et al.* (2000)	< 1 000	no	mangroves were not widespread in the recent past in Leschenault Inlet
recent fossil sediment, under deltaic shoals of the Preston River delta, where there are mangrove nearby today See Semeniuk *et al.* (2000)	< 1 000	no	mangroves were not widespread in the recent past in Leschenault Inlet
fossil sediment at 2 sites under stranded tidal flats, Peel-Harvey estuary(Transect 3 of Semeniuk & Semeniuk [1991) and Transect 8 of Semeniuk & Semeniuk [1990]); no mangroves today	7 000-4 500	no	mangroves were absent from the Peel-Harvey Estuary, and thus were not more widespread along coast earlier in Holocene
fossil sediment under stranded tidal flats, Swan River Estuary (3 sites, in the upper to middle estuary *viz* Redcliffe Bridge, Garrat Road Bridge, and Ellam Street Jetty); no mangroves today	no date	no	mangroves were absent from the Swan River, and thus were not more widespread along coast earlier in Holocene
fossil sediment under river channel at 60 m below MSL (Churchill 1959); no mangroves today	12 000	no	though Churchill described the pollen-bearing sediment as a freshwater peat, the site was situated at depth along the valley tract of the Swan River, and potentially was the upland part of the Swan River estuary; if this is the case, it appears that mangroves were not present within Swan River estuary in the early Holocene

Inlet mangroves in a western transitional division named from the presence of the key species, *Avicennia marina* and *Halocarcia indica bidens* which extends from Leschenault Inlet to Shark Bay. If the hypothesis that *Avicennia marina* at Leschenault Inlet is linked to the mangroves of the Houtman Abrolhos Islands and Carnarvon/Gascoyne region via the Leeuwin Current is correct, then perhaps *Avicennia* at all these locations should be viewed as deriving from a single species pool, and should be regarded as a single biogeographic region. This accords with the classification presented in Bridgewater & Cresswell (1999). If, on the other hand, the hypothesis that *Avicennia marina* at Leschenault Inlet is truly a relict outlier, isolated from its tropical sympatriates for the latter part of the Holocene by a shifting climate, then perhaps the Leschenault Inlet and the Carnarvon/Gascoyne populations should be regarded now as separate biogeographic regions. Resolution of these questions must await further research, particularly into genetic comparisons of the populations. Bridgewater & Cresswell (1999) recognise 11 biogeographic divisions for mangrove and saltmarsh vegetation in Australia, and note that these compare well with regions derived from a broader set of attributes for the Interim Marine and Coastal Regionalisation for Australia.

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Contemporary and sub-recent pollen record for the Leschenault Inlet estuary: towards a palynological baseline

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Abstract

Palynological analysis of contemporary and sub-recent sediments from Leschenault Inlet, an estuarine lagoon on the south-west coast of Western Australia, has determined if a contemporary palynological baseline can be established to interpret the sub-recent pollen assemblages, and was used to determine the mangrove *Avicennia marina* was a component of the vegetation in the recent past. Leschenault Inlet is a relatively simple estuarine system with north-south trending sedimentary environments and parallel vegetation complexes, and with both easterly and westerly winds and two fluviatile sources contributing to the pollen influx. Using predominantly family groupings (*e.g.* Chenopodiaceae, Myrtaceae, Casuarinaceae, Gramineae, Restionaceae) and several species prominent in the vegetation (*Frankenia pauciflora, Olearia axillaris, Lepidosperma gladiatum*), preliminary results indicate that the major sedimentary environments have characteristically different pollen assemblages. In transects across the sedimentary environments, individual species show relative abundance gradients that can be explained in terms of proximity to vegetation source and potential transport systems. Conversely, these serve to distinguish specific environments and the nature of the immediate upland source vegetation. *Avicennia marina* pollen is a minor component of the contemporary sediments near sites of mangrove habitation. It is absent from sub-recent samples in comparative environments, implying that it is a recent arrival to Leschenault Inlet. A late Holocene change in climate may be responsible for an intensification of the Leeuwin Current and subsequent delivery of *Avicennia* propagules from tropical regions. Leschenault Inlet is an excellent site to study the effect on palynological assemblages of proximity to vegetation source, wind directions, dispersal via estuarine currents, and taphonomy. It also presents an ideal setting from which to develop pollen assemblage baselines for the different estuarine sedimentary environments. From a geoheritage perspective, the Leschenault Inlet estuary probably ranks as significant at a national level.

Keywords: estuarine palynology, palynology, Leshenault Inlet, south-western Australia.

Introduction

Leschenault Inlet is a north-south trending estuarine lagoon situated on the southwest coast of Western Australia. It is barred by a long barrier dune system, the Leschenault Peninsula, and has a range of depositional (accretionary) environments and pollen-source habitats (both oriented north-south), an east-west to southwesterly aeolian delivery system, and two southerly located fluvial delivery systems. The estuarine sedimentary fill is entirely Holocene in age, and in the context of a retrograding barrier a complete estuarine sedimentary record from *ca* 8 000 yrs BP to the present is preserved (Semeniuk 1985). Considering its depositional setting, Leschenault Inlet estuarine lagoon potentially contains a valuable palynological record of Holocene environments.

The diverse range of habitats that border the estuarine system supports a mosaic of vegetation complexes that range from saltmarsh to freshwater terrestrial associations. Of particular interest is the presence of the mangrove *Avicennia marina*, a species that is otherwise not known south of Houtman Abrolhos. *Avicennia marina* is a potential indicator of past Holocene climates and environments, and it has been suggested anecdotally that this isolated stand of a normally tropical species represents a relict population. However, it is also possible that *A. marina* is a recent arrival, its propagules having been transported by an intensified Leeuwin Current.

To adequately interpret the sub-recent pollen record in the estuarine sediments, a baseline of pollen assemblages in the various contemporary sedimentary suites or facies is required. This paper provides a preliminary account of the pollen record preserved in contemporary (surface) sediments and the upper parts of the Holocene sedimentary sequence (= sub-recent *viz* from 150 yrs BP to 500-1500 yrs BP) in Leschenault Inlet (Fig 1).

The specific objectives of this paper are: to characterise the pollen record in the surface sediments of the five main sedimentary suites (or facies) in the estuary, and from these interpret the pre-modern Holocene stratigraphic record; to determine the extent and mode of pollen trans-

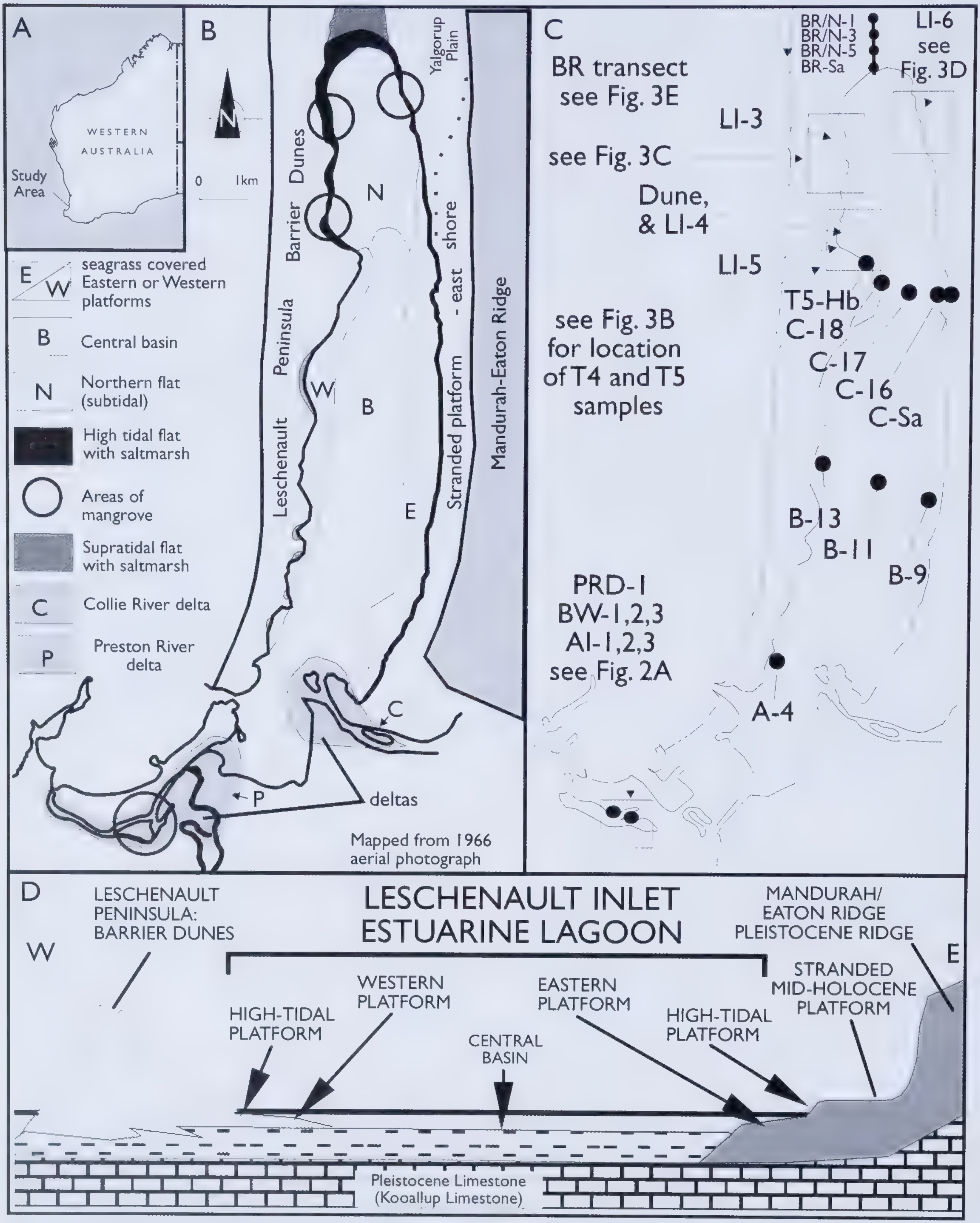

Figure 1. Leschenault Inlet showing location of main sedimentary/ geomorphic units, sampling sites, locations of detailed study areas, and Holocene stratigraphic framework.

port from its source, and to determine if *Avicennia* pollen is present in the sub-recent stratigraphic record. The general patterns in the contemporary and sub-recent pollen assemblages will provide preliminary conclusions and point the way for future more detailed studies of the pollen record and factors that influence its composition.

Setting

Estuarine sedimentary environments

Leschenault Inlet is an estuarine lagoon located along the Western Australian coast within the southern part of the Swan Coastal Plain (Fig 1; Semeniuk & Meagher 1981a). The lagoon is separated from the Indian Ocean by a barrier dune system, the Leschenault Peninsula (Semeniuk 1985). To the east, it onlaps the Mandurah-Eaton Ridge and the Yalgorup Plain (Semeniuk 1997).

The Leschenault Peninsula is a linear, north-south oriented dune barrier 0.5 to 1.0 km wide, and is comprised of east-west oriented mobile to vegetated parabolic dunes (Semeniuk & Meagher 1981a; Semeniuk *et al.* 1989). The Mandurah-Eaton Ridge is a high ridge of quartz sand and limestone, oriented north-south and bordering the eastern margin of the Holocene estuarine complex (Semeniuk 1997). Leschenault Inlet is an elongate, narrow, north-south oriented estuarine lagoon approximately 1.5 to 2.5 km wide, and 13 km long (Wurm & Semeniuk 2000). Bordering its eastern shore is a stranded sand platform 1-2 m above sea level, formed earlier in the Holocene as a sub-aqueous estuarine sand platform. The depositional units of interest in this paper are the central basin, the eastern and western platforms, the high-tidal platform, the supratidal flat, and the Preston River delta. The characteristics of these units are described briefly in Table 1. The main estuarine geomorphic and sedimentary units within Leschenault Inlet, and the Quaternary stratigraphy of the area (after Semeniuk 1983, 1997), are illustrated in Fig 1D.

Table 1. Description of geomorphic/sedimentary units in Leschenault Inlet selected for study in this paper

Geomorphic/ sedimentary unit	Description
central basin	long, shore-parallel relatively deep water mud-floored depression, generally 1.5-2.0 m deep
eastern platform	shore-parallel narrow, shallow water sand platform (low tidal to 1.0 m deep), vegetated by the seagrass *Halophila ovalis*
western platform	shallow water muddy sand platform or ramp (low tidal to 1.5 m deep), also vegetated by *Halophila ovalis*
high-tidal platform	high-tidal platforms located on the east and west shores of the estuarine lagoon; width varies from narrow (5-10 m) to wide (>500 m); mainly saltmarsh-vegetated
supratidal flat	broad flat, nearly horizontal, to very gently inclined towards the estuary, emergent by progradation, underlain by mud, and colonised by samphire; borders the northern estuary
Preston River delta	complex of linear, tidal-current-aligned shoals and emergent islands, with intervening shallow channels

Vegetation contributing pollen

There are nine main categories of vegetation that may act as pollen sources for the estuarine sediments: barrier dune vegetation; Mandurah-Eaton Ridge vegetation; Yalgorup Plain vegetation; supratidal vegetation on emergent deltaic shoals; freshwater vegetation on the east shore of the estuary; saltmarsh vegetation fringing the shore of the estuary; mangrove vegetation along the shore of the estuary; seagrass vegetation; and exotic vegetation. The locations of these polen sources are shown in Fig 2.

The barrier dunes are comprised of a mosaic of habitat types and vegetation (Semeniuk & Meagher 1981a,b; Trudgeon 1984; Cresswell & Bridgewater 1985; Smith 1985; Semeniuk *et al.* 1989). Semeniuk & Meagher (1981b) categorised the vegetation on the barrier in relation to the main landforms (or habitats), recognising four broad assemblages: 1. *Olearia* scrub assemblage, with *Olearia axilaris, Rhagodia bacatta, Spyridium* sp, *Acacia rostellifera,* and *A. cyclops* inhabiting recently fixed dunes; 2. *Acacia* scrub assemblage, with *Acacia rostellifera, A. cyclops,* and *Agonis flexuosa* inhabiting older fixed dunes; 3. the peppermint low forest assemblage, with *Agonis flexuosa,* inhabiting geomorphically degraded dunes; and 4. the tuart woodland assemblage with *Eucalyptus gomphocephala, Agonis flexuosa, Hakea prostrata, Acacia rostellifera,* and *A. cyclops* inhabiting swales in the dunes. Other species generally occurring in the dunes include *Hibbertia cuneiformis, Jacksonia furcellata, Trachyandra divaricata, Acacia saligna, Isolepis nodosa, Apium prostratum,* and *Lepidosperma gladiatum.*

On the quartz sand high ground of the Mandurah-Eaton Ridge the vegetation comprises a mosaic of assemblage types (Heddle *et al.* 1980). Key species in this system include *Eucalyptus calophylla* and *E. marginata, Allocasuarina fraseriana,* Proteaceae (various species of *Banksia* and *Isopogon, Stirlingia latifolia, Xylomelum occidentale*), *Kunzea ericifolia, Macrozamia reidlei,* and *Hibbertia hypericoides.* On the low limestone and quartz sand plain of the Yalgorup Plain, key species include *Eucalyptus gomphocephala, E. calophylla, Allocasuarina fraseriana, Banksia attenuata, Macrozamia reidlei,* and *Hibbertia hypericoides.* Vegetation on the emergent supratidal deltaic shoals in the Preston River delta complex (Semeniuk 2000), equivalent to the sandy rise complex of Pen *et al.* (2000), may be comprised of *Jacksonia furcellata, Casuarina obesa, Hakea prostrata, Acacia saligna, A. cyclops, A. cochlearis, Viminaria juncea, Hibbertia cuneiformis, Sporobolus virginicus,* and *Isolepis nodosa.*

Freshwater vegetation inhabits the broad wetland complex on the eastern shore of the estuary. This zone is a low level platform, formed as a stranded mid-Holocene subtidal

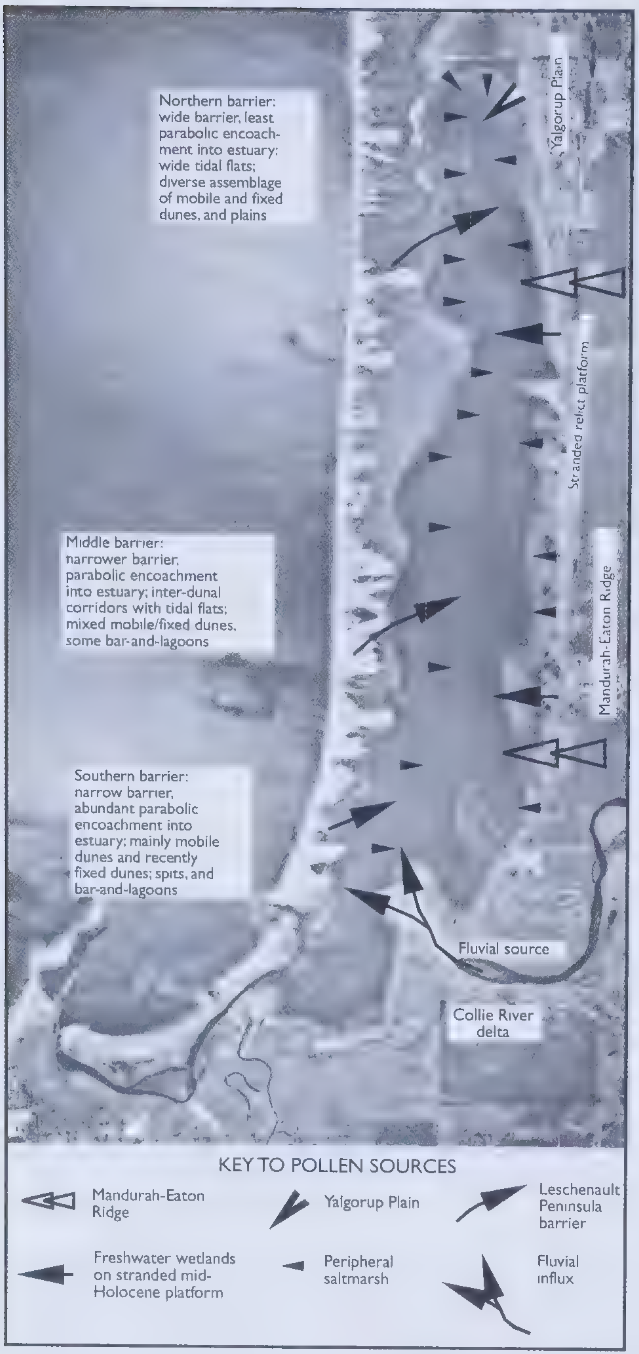
Northern barrier: wide barrier, least parabolic encoachment into estuary; wide tidal flats; diverse assemblage of mobile and fixed dunes, and plains
Yalgorup Plain
Stranded relict platform
Middle barrier: narrower barrier, parabolic encoachment into estuary; inter-dunal corridors with tidal flats; mixed mobile/fixed dunes, some bar-and-lagoons
Mandurah-Eaton Ridge
Southern barrier: narrow barrier, abundant parabolic encoachment into estuary; mainly mobile dunes and recently fixed dunes; spits, and bar-and-lagoons
Fluvial source
Collie River delta
KEY TO POLLEN SOURCES
Mandurah-Eaton Ridge
Yalgorup Plain
Leschenault Peninsula barrier
Freshwater wetlands on stranded mid-Holocene platform
Peripheral saltmarsh
Fluvial influx

Figure 2. Aerial photograph of the Leschenault Inlet area showing main vegetation systems and the pollen sources.

estuarine platform (Pen *et al.* 2000; Semeniuk 2000). The most widespread and dominant species is *Melaleuca rhaphiophylla*. Also occurring in this habitat are *Eucalyptus rudis*, *Baumea juncea*, *Agonis flexuosa*, *Acacia saligna*, *Hemarthria uncinata*, *Baumea articulata*, *Lepidosperma longitudinale*, *L. gladiatum* and *Juncus pallidus*. Towards its contact with the present estuarine shore, the wetland complex surface is inhabited by *Melaleuca cuticularis*, *M. viminea*, and *Casuarina obesa*. Local areas emergent above the watertable support *Eucalpytus gomphocephala*.

Saltmarsh vegetation occurs as low herbland formations around the periphery of Leschenault Inlet. The species that comprise these formations include. *Halosarcia indica bidens*, *Halosarcia halocnemoides*, *Salicornia quinqueflora*, *Suaeda australis*, *Polypogon monspelliensis*, *Sporobolus virginicus*, *Samolus repens*, *Sarcocornia quinqueflora*, *Bulboschoenus caldwellii*, and *Frankenia pauciflora* (Pen *et al.* 2000). The white mangrove *Avicennia marina* forms scrub and heathland (following Specht 1970) in local areas around the shores of the estuary (Fig 3). Seagrass vegetation (*i.e.* aquatic estuarine/marine vegetation) forms shallow water meadows in Leschenault Inlet, and includes *Halophila ovalis*, *Heterozostera megacarpa*, and *Ruppia tasmanica*.

Exotic vegetation (*i.e.* alien species) in the region that may contribute pollen to the Leschenault Inlet estuary include. pine plantations (*Pinus radiata* and *P. pinaster*), blue gum plantations (*Eucalyptus globulus*), crop, horticultural, and garden plants (*e.g. Lupinus*), and weeds such as couch grass (*Cynodon dactylon*), kikuyu (*Pennisetum clandestinum*), Paspalum grass (*Paspalum vaginatum*), and pigface (*Carpobrotus edulis*). Generally, the pines, blue gums, and crop, horticultural, and garden plants are located to the east of Leschenault Inlet, so that the occurrence of their pollen in estuarine sediments signals transport from eastern sources. Weeds also are mainly located to the east of Leschenault Inlet in residential areas, pasture land, and on the Collie River delta.

Given this range of contributing vegetation there are a number of mechanisms that result in anemophilous (rather than entomophilous) pollen being emplaced in the estuarine environment. These are: transport by wind, (by seabreezes transporting pollen from the western barrier dune vegetation, saltmarsh, and mangrove formations, and by landbreezes transporting pollen from the eastern Mandurah-Eaton Ridge, saltmarsh vegetation, and from peripheral freshwater vegetation; and locally from the emergent deltaic shoals); transport within the estuary by currents, including later re-working of previously deposited pollen; transport by wind and/or rivers from the east from a variety of hinterland vegetation formations, and delivered to the estuary by fluvial current within and proximal to the deltas; transport by avifauna (this may be a minor transport mechanism); and *in situ* accumulations.

The range of source species, transporting media, and transportation directions would appear to complicate the palynological records. However, the large-scale geomorphic units in the area have diagnostic vegetation assemblages, and thus a single species or group of species can signal derivation from a particular habitat. For instance, *Banksia* does not occur on the dune barrier, nor on the saltmarshes; *Olearia* does not occur on the Mandurah-Eaton Ridge or on the saltmarshes; and *Halosarcia* spp specifically inhabit only the saltmarshes. In this context, there are key species that are diagnostic of source environment (Table 2).

Pollen vectors: wind, currents and runoff

The three main vectors for transporting pollen in the Leschenault Inlet system are wind, estuarine currents, and fluvial run-off. Estuarine currents in the Leschenault Inlet estuary are driven by wind and tides. Wind waves rework the muddy sediment of the platforms, and under the effect of a northward net current, deposit mud in the deep water of the central basin or in the northern parts of the estuary (Semeniuk 2000). Any pollen delivered to the platforms potentially can be reworked under these conditions, and redeposited along with mud particles in the sites of mud accumulation.

The Collie River and the Preston River discharge freshwater into the estuary, and their drainage basins potentially draw on pollen material delivered by *in situ* fall from riparian vegetation, eroded from soils in the hinterland that support a variety of vegetation types, and reworked wind-delivered material (*e.g.* pine pollen raining down on the drainage basin and floodplains of the rivers). All such pollen, through fluvial reworking and transport, can find its way into the Leschenault Inlet estuary.

Wind patterns, and their strength and direction in relation to anemophilous plant flowering times, are critical factors in determining the types of pollen and the amount of pollen that is delivered to the depositional environment. The Leschenault Inlet area is characterised by three wind patterns (Semeniuk & Meagher 1981a). a summer pattern of landbreezes and seabreezes, a prevailing winter pattern, and a winter-storm pattern. The pattern in spring is transitional between winter and summer patterns, with easterlies and the landbreeze/seabreeze system progressively intensifying. The wind patterns of interest are those that occur during the flowering season, from August to November, and for some species progressing to February.

It is important to note that other factors may contribute to the composition of a pollen assemblage. For example, prolific anemophilous plants on the Mandurah-Eaton Ridge, flowering at a time of calm or weak easterly winds in say, August, may not deliver as much pollen to the sedimentary repository as a less prolific pollen-producing plant flowering at a time of strong easterly winds in summer. Also, there may be prolific entomophilous pollen production, which may be preserved *in situ*, but this would have a negligible contribution via winds. A full analysis of the flowering times of anemophilous and entomophilous plants, their location, their abundance, the wind speeds and direction at times of plant flowering, and the abundance of their pollen within Leschenault Inlet, however, is beyond the scope of this study.

The saltmarsh plants *Frankenia pauciflora, Halosarcia indica bidens, H. halocnemoides, Sarcocornia quinqueflora,* and *Suaeda australis* flower at various times of the year (Marchant *et al.* 1987). In addition to wind dispersal *in situ* accumulations of pollen on the tidal flat are dispersed by estuarine currents to sub-aquatic platforms and the central basin. For *Avicennia marina,* which commences flowering in March-May (Semeniuk *et al.* 1978), *in situ* accumulation and subsequent estuarine current dispersion are significant factors.

Methods

Samples were collected from the undisturbed sedimentary surface of estuarine and saltmarsh environments, and from stratigraphic profiles (Fig 3). Sampling sites were selected from the 22 sites of Wurm & Semeniuk (2000), across the estuary to illustrate across-estuary trends. Contemporary environments sampled include the mangrove zone, sub-aquatic estuary platform (B9, 13, and C16, 18), estuarine basin (B11, C17), and saltmarsh zone. Pen *et al.* (2000), Wurm & Semeniuk (2000), and Semeniuk (2000) provide general descriptions of the settings of these sites.

Table 2. Diagnostic key species of the source environment for Leschenault Inlet

Large scale habitat setting	Key species diagnostic to the setting
Barrier dunes	*Acacia cyclops, A. rostellifera, Eucalyptus gomphocephala, Olearia axillaris, Rhagodia bacatta*
Mandurah-Eaton Ridge	*Banksia* spp, *Eucalpytus calophylla, Eucalyptus marginata, Isopogon* spp, *Kunzea ericifolia, Stirlingia latifolia*
Yalgorup Plain	*Eucalyptus gomphocephala, Eucalyptus calophylla*
emergent deltaic shoals	*Casuarina obesa, Hakea prostrata, Viminaria juncea*
freshwater to saltwater wetlands, east shore	*Baumea articulata, Baumea juncea, Melaleuca cuticularis, M. rhaphiophylla, M. viminea*
saltmarsh	*Frankenia pauciflora, Halosarcia indica bidens, H. halocnemoides, Juncus kraussii, Salicornia quinqueflora, Suaeda australis*
mangrove	*Avicennia marina*
seagrass	*Halophila ovalis, Heterozostera, Ruppia megacarpa, Zostera muelleri*
exotic plants	*Pinus radiata, P. pinaster, Eucalyptus globulus, Lupinus* spp, *Cynodon dactylon, Pennisetum clandestinum, Paspalum vaginatum, Carpobrotus edulis*

The stratigraphic samples, collected to investigate the sub-recent (very late Holocene) occurrence of *Avicennia marina,* were obtained from (Fig 3): 1. the Preston River delta, where mangroves are currently extant; 2. the sub-surface muds in the vicinity of mangroves at Site LI-4B; 3. the sub-surface muds in the vicinity of mangroves at Site LI-6; and 4. along a north-south oriented transect across supratidal flats in northern Leschenault Inlet. The sampling strategy for these sub-recent stratigraphic settings was designed to target the zone of most likely occurrence of mangrove pollen , if indeed mangroves were present at that time.

Pollen and spore assemblages were recovered from the sediments following the extraction techniques of Phipps & Playford (1984). Residue strew mounts from thirty two samples in total were microscopically examined. All samples were scanned for the presence of *Avicennia marina* pollen, 12 samples were counted to characterise the pollen assemblages from different contemporary depositional environments, and nine of the sub-recent samples were counted for comparison with the contemporary assemblages. Table 3 lists all samples, their stratigraphic location/

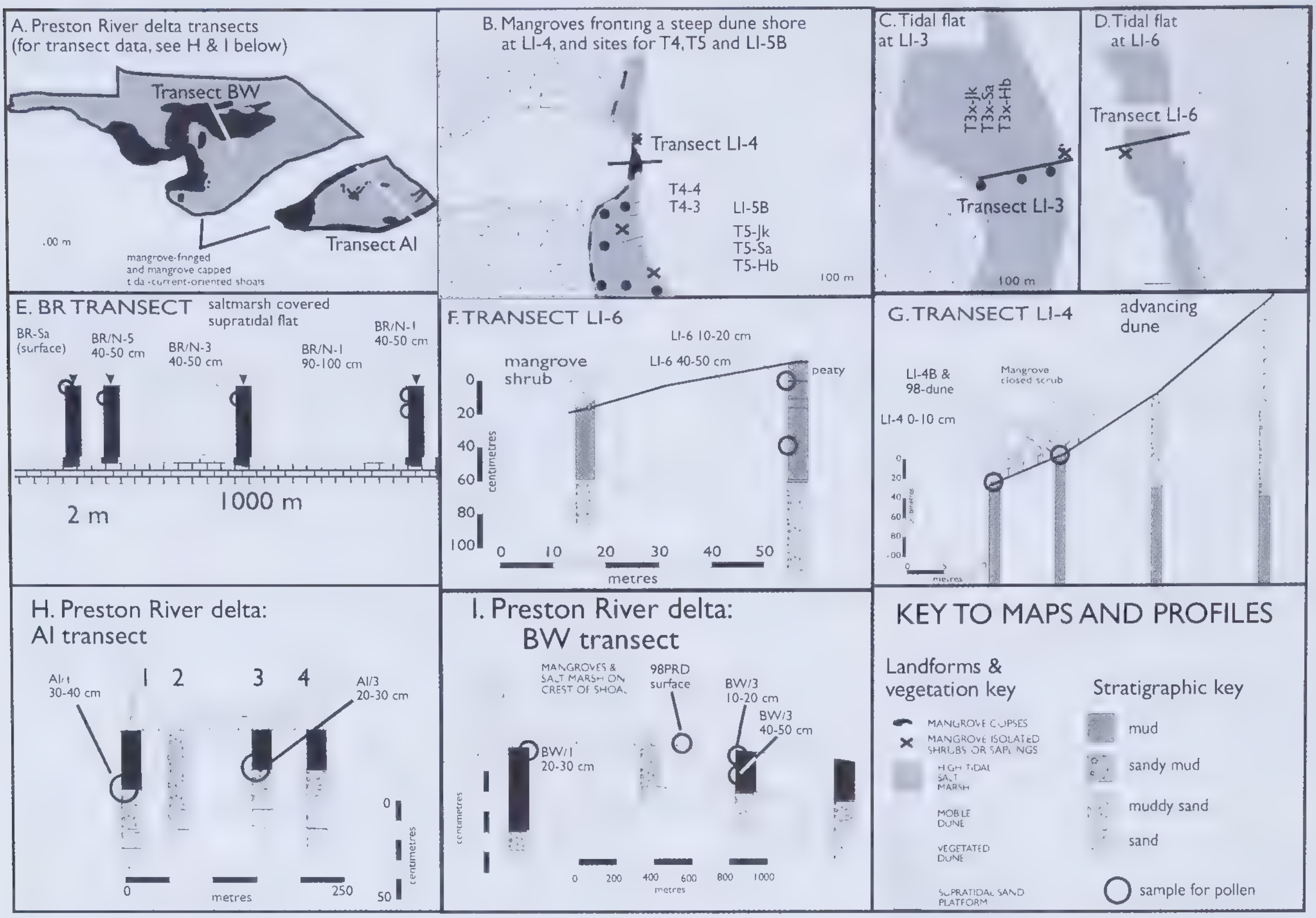

Figure 3. Location of transects and study sites in study areas, and stratigraphic setting and location of pollen samples.

environment, rationale for sampling, type of palynological analysis, and the presence or absence of *Avicennia marina* pollen.

Modern pollen reference slides were prepared from acetolysed pollen samples collected from fourteen critical species in the local flora, and *Avicennia marina* pollen was obtained from specimens mounted on herbarium sheets held at the Western Australia Herbarium. A range of pollen which are thin-walled did not survive the acetolysis process *i.e. Juncus kraussii* (Juncaceae) and the seagrasses *Halophylla ovalis, Heterozostera* sp, *Ruppia megacarpa,* and *Zostera muelleri,* and consequently are not recorded in the pollen assemblages.

Pollen counts

In the pollen counts, species identification was carried out where possible and critical, but the majority of specimens were identified only to the generic or family level. Pollen from the five species of Chenopodiaceae sampled from the local vegetation were grouped together because their differing preservation in the samples made it difficult to reliably differentiate between species. Similarly, pollen of Myrtaceae are grouped together in the analysis, but the dominance of *Eucalyptus* over the *Melaleuca/Agonis* group in particular samples is referred to where appropriate. *Pinus* was the main exotic palynomorph readily identified in the samples. Other potential exotic pollen, from *Eucalyptus globulus* and grasses such as *Cynodon dactylon, Pennisetum clandestinum.* and *Paspalum vaginatum* were not differentiated from native species. The total percent occurrence of taxa counted in each sample is listed in Table 4. To characterise and compare the pollen assemblages from each site, *Pinus* pollen was removed and minor taxa further grouped. Note that in these analyses the data are presented as relative percentages, and not as absolute numbers for a given volume of sediment.

Scans for *Avicennia marina* pollen

For each sample, one to two strew slides were scanned for the presence of *Avicennia marina* pollen. For samples rich in palynomorphs, up to 15 000 pollen grains were included in the scan. For the rare samples depauperate in palynomorphs, only several hundred grains were scanned.

Avicennia marina pollen grains are tricolporate and oblate spheroidal with distinct colpi and circular pores averaging 10 mm in diameter. Colpi terminate sharply and have a distinctive psilate colpal membrane. Grains are sculpturally reticulate with prominent but short columellae, the expanded heads of which are fused to form the 1 µm wide muri; lumina are irregular and as thick as, or thinner than, the muri. Pollen of *A. marina* has an average polar diameter of 26 µm and an average equatorial diameter of 29 µm.

The tricolporate/colpate pollen group listed in the relative percent occurrence of species (Table 4) includes several types that, without close examination, could be mistaken for *A. marina* pollen. The large pores, prominent colpal membranes, and distinctive reticulum of *A. marina* pollen serve to differentiate it from the other tricolporate types in the Leschenault Inlet samples.

Results

Pollen groups and species identified in this study are as follows: 1) identification to Family level: Casuarinaceae, Chenopodiaceae, Compositae, Gramineae, Liliaceae, Myrtaceae, Proteaceae (excluding *Isopogon* and *Stirlingia*), and Restionaceae; 2) identification to genus level: *Gonocarpus, Isopogon, Ligularia?, Pinus,* and *Stirlingia;* 3) identification to species level: *Acacia cyclops, Aprum prostratum, Avicennia marina, Frankenia pauciflora, Lepidosperma gladiatum,* and *Olearia axillaris;* and 4) indeterminate identification: Dicotyledons, Tricolporate/colpate gen indet, Dicotyledon Gen. *et* sp indet, Cryptogam spores, Hepaticae (?*Phaeoceros*), Selaginellaceae, and Gen *et* sp indet. The results of the pollen counts are presented in Table 3 to 5.

Pollen assemblages

Gramineae and Casuarinaceae pollen are relatively consistent and show no trends in relative abundance in the main sedimentary environments (*viz* the saltmarsh, the western platform, the central basin, and the eastern platform).

Pollen assemblages in the saltmarsh environment on the western shore are dominated by Chenopodiaceae. The native pollen assemblages from the sub-aquatic western platform, central basin, and sub-aquatic eastern platform environments are similar in being dominated by Myrtaceae,

Table 3. Samples studied, rationale for study, pollen counts (NB. all samples were scanned), and presence of mangrove (*Avicennia marina*) pollen.

Sampling rationale	**Samples (environment)**	**Pollen count**	**Mangrove pollen present**
	Contemporary samples		
Presence of mangrove pollen; typify pollen assemblage	LI-4B 10 cm (mangrove zone)	Yes	Yes
	98-dune surface (mangrove zone)		Yes
	98 PRD surface (mangrove zone)	Yes	Yes
Typify pollen assemblages across estuary; presence of mangrove pollen	A4 (subaquatic estuary platform)		No
	C9 (subaquatic estuary platform)	Yes	No
	C11 (estuarine basin)	Yes	No
	C13 (subaquatic estuary platform)	Yes	No
	B16 (subaquatic estuary platform)	Yes	No
	B17 (estuarine basin)	Yes	Yes
	B18 (subaquatic estuary platform)		No
	C-Sa (saltmarsh)	Yes	No
Typify saltmarsh pollen assemblages; presence of mangrove pollen	Br-Sa (saltmarsh)	Yes	No
	T3x-5C (saltmarsh)		No
	T3x-Hb (H. indica bidens zone)		No
	T3x-Jk (Juncus kraussii zone)		Yes
	T4-3 (saltmarsh)		Yes
	T4-4 (saltmarsh)		No
	LI-5B 10 cm (saltmarsh)		No
	T5-Sa (saltmarsh)		No
	T5-Hb (H. indica bidens zone)	Yes	No
	T5-Jk (Juncus kraussii zone)		No
	Stratigraphic samples		
Determine if mangrove pollen present in subrecent sediments under extant mangrove sites, or nearby	AI/1 30-40 cm (Preston River delta)		No
	AI/3 20-30 cm (Preston River delta)	Yes	No
	BW/1 20-30 cm (Preston River delta)	Yes	No
	BW/3 10-20 cm (Preston River delta)	Yes	No
	BW/3 40-50 cm (Preston River delta)	Yes	No
determine if mangrove pollen present in subrecent sediments under extant mangrove sites or nearby	LI-6 10-20 cm (saltmarsh, NE inlet)		No
	LI-6 40-50 cm (saltmarsh NE inlet)	Yes	
	BR/N-1 40-50 cm (northern supratidal flat)	Yes	No
	BR/N-1 90-100 cm (northern supratidal flat)	Yes	No
	BR/N-3 40-50 (northern supratidal flat)	Yes	No
	BR/N-5 40-50 cm (northern supratidal flat)	Yes	No

Table 4. Pollen counts for species/groups found in sites sampled in Leschenault Inlet estuary (250 grain count).

TAXA SITES	A4	B9	B11	B13	C16	C17	C18	Br-Sa	T5-Hb	PRD surf	A1/3 20-30	BW/1 20-30	BW/3 10-20	LI-4B 0-10	LI-5B 0-10	BR/N/ 3 40-50	BR/N/ 5 40-50	BR/N/1 90-100	LI-6 40-50
Casuarinaceae	20	19	33	26	16	30	15	1	7	11	-	-	-	7	4	4	13	29	15
Myrtaceae	52	114	103	52	87	65	86	16	46	69	2	14	12	11	23	10	102	95	23
Gramineae	29	58	54	40	33	41	36	12	15	39	-	9	7	20	10	25	7	22	5
Pinus	73	8	4	31	17	33	21	9	10	11	-	-	-	137	5	3	1	2	0
Avicennia marina	-	-	-	-	-	3	-	-	4	6	-	-	-	-	-	-	-	-	0
Chenopodiaceae	19	29	20	24	86	36	59	201	152	94	238	194	231	52	200	140	20	39	183
Lepidosperma gladiatum		2		6	1	7	1	-	-	-	-	-	-	2	-	50	10	10	6
Restionaceae	10	3	7	6	3	11	8	5	2	-	-	1	-	4	1	1	7	15	1
Compositae	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Olearia axillaris	7	1	6	10	2	10	2	2		6	3	-	-	4	1	1	73	3	4
Ligularia?	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Frankenia pauciflora	1	4	1	-	-	1	1	-	-	-	6	-	-	-	-	-	-	-	0
Aprum prostratum	-	-	1	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	0
Gonocarpus	2	-	4	5	-	-	2	-	-	-	-	-	-	1	-	-	-	4	0
Isopogon	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Proteaceae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Acacia cyclops	-	-	-	1	-	-	1		2	-	-	-	-	-	-	-	-	2	1
Gen et sp indet	11	-	6	9	-	3	4	4	4	1	1	1	-	6	-	-	4	8	3
Tricolporate/colpate gen. indet.	5	4	3	10	2	4	4	-	8	8	-	26	-	2	3	8	-	8	8
Stirlingia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Liliaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	0
CRYPTOGAM SPORES																			
Hepaticae (?Phaeoceros)	7	-	4	14	1	2	7	-	-	2	-	-	-	1	-	2	1	1	0
Selaginellaceae	-	1	-	-	-	1	-	-	-	1	-	-	-	-	-	-	10	1	0
Gen et sp indet	8	7	2	14	2	3	3	-	1	2	-	4	-	3	-	5	2	7	1

Table 5. Percentage occurrence of pollen of species/groups sampled in Leschenault Inlet estuary.

TAXA SITES	A4	B9	B11	B13	C16	C17	C18	Br-Sa	T5-Hb	PRD surf	A1/3 20-30	BW/1 20-30	BW/3 10-20	LI-4B 0-10	LI-5B 0-10	BR/N/3 40-50	BR/N/5 40-50	BR/N/1 90-100	LI-6 40-50
Casuarinaceae	8	7.6	13.2	10.4	6.4	12	6	0.4	2.8	4.4	0	0	0	2.8	1.6	1.6	5.2	11.6	6
Myrtaceae	20.8	45.6	41.2	20.8	34.8	26	34.4	6.4	18.4	27.6	0.8	5.6	4.8	4.4	9.2	4	40.8	38	9.2
Gramineae	11.6	23.2	21.6	16	13.2	16.4	14.4	4.8	6	15.6	0	3.6	2.8	8	4	10	2.8	8.8	2
Pinus	29.2	3.2	1.6	12.4	6.8	13.2	8.4	3.6	4	4.4	0	0	0	54.8	2	1.2	0.4	0.8	0
Avicennia marina	0	0	0	0	0	1.2	0	0	1.6	2.4	0	0	0	0	0	0	0	0	0
Chenopodiaceae	7.6	11.6	8	9.6	34.4	14.4	23.6	80.4	60.8	37.6	95.2	77.6	92.4	20.8	80	56	8	15.6	73.2
Lepidosperma gladiatum	0	0.8	0	2.4	0.4	2.8	0.4	0	0	0	0	0	0	0.8	0	20	4	4	2.4
Restionaceae	4	1.2	2.8	2.4	1.2	4.4	3.2	2	0.8	0	0	0.4	0	1.6	0.4	0.4	2.8	6	0.4
Compositae gen. et sp. indet	2.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Olearia axillaris	2.8	0.4	2.4	4	0.8	4	0.8	0.8	0	2.4	1.2	0	0	1.6	0.4	0.4	29.2	1.2	1.6
Ligularia ?	0	0	0.4	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frankenia pauciflora	0.4	1.6	0.4	0	0	0.4	0.4	0	0	0	2.4	0	0	0	0	0	0	0	0
Apium prostratum	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	1.2	0	0	0	0
Gonocarpus	0.8	0	1.6	2	0	0	0.8	0	0	0	0	0	0	0.4	0	0	0	1.6	0
Isopogon	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proteaceae gen. indet.	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acacia cyclops	0	0	0	0.4	0	0	0.4	0	0.8	0	0	0	0	0	0	0	0	0.8	0.4
Gen et sp indet	4.4	0	2.4	3.6	0	1.2	1.6	1.6	1.6	0.4	0.4	0.4	0	2.4	0	0	1.6	3.2	1.2
Tricolporate/colpate gen. indet.	2	1.6	1.2	4	0.8	1.6	1.6	0	3.2	3.2	0	10.4	0	0.8	1.2	3.2	0	3.2	3.2
Stirlingia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liliaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	1.6	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
CRYPTOGAM SPORES																			
Hepaticae (?Phaeoceros)	2.8	0	1.6	5.6	0.4	0.8	2.8	0	0	0.8	0	0	0	0.4	0	0.8	0.4	0.4	0
Selaginellaceae	0	0.4	0	0	0	0.4	0	0	0	0.4	0	0	0	0	0	0	4	0.4	0
Gen et sp indet	3.2	2.8	0.8	5.6	0.8	1.2	1.2	0	0.4	0.8	0	1.6	0	1.2	0	2	0.8	2.8	0.4

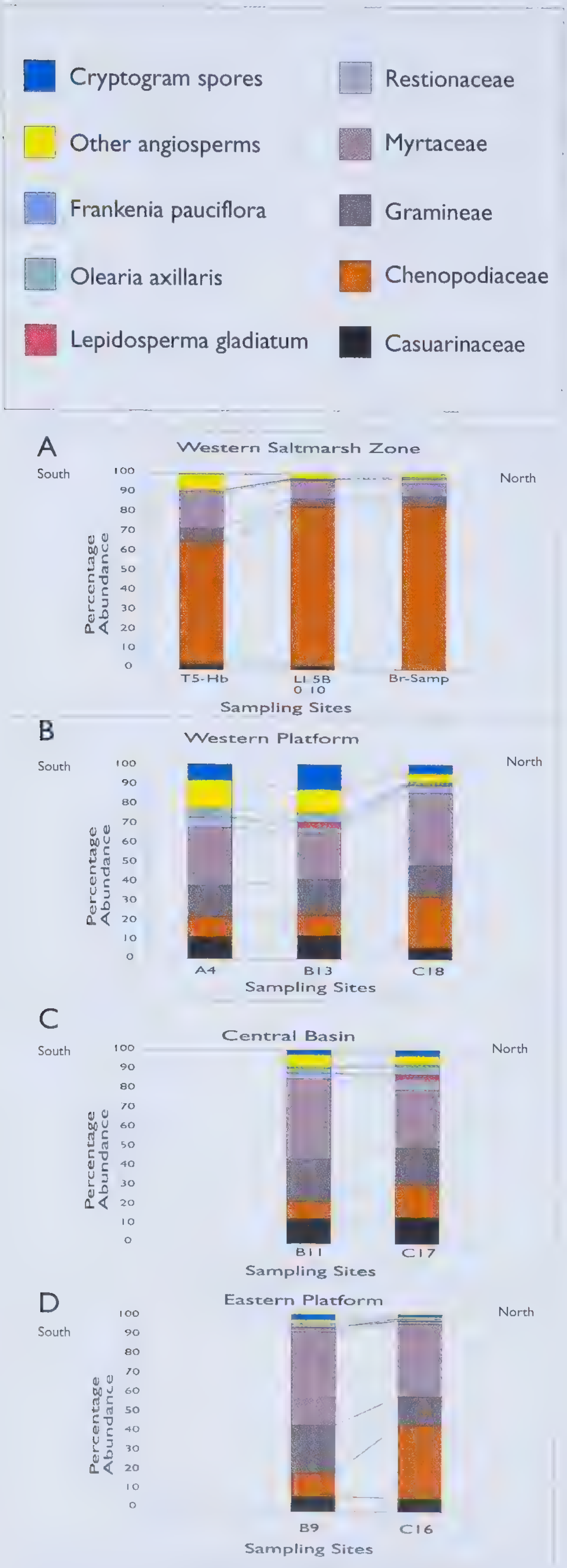

Figure 4. Occurrence of pollen of selected/species groups from the contemporary surfaces of the western saltmarsh zone, western platform, central basin, and eastern platform.

Chenopodiaceae, Gramineae, and Casuarinaceae (Fig 4). In each of these environments Chenopodiaceae pollen show a south to north increase in abundance, reflecting the increase in abundance of parent plants towards the northern tidal saltmarsh flats. *Olearia axillaris* pollen is most common in the southern and central sites on the western sub-aquatic platform and in the central basin, but is rare in the eastern sub-aquatic platform environment. This distribution reflects the proximity of the mobile and recently fixed dune habitats in the southern and middle Leschenault Peninsula barrier, a habitat that *Olearia axillaris* prefers. The relative prominence of this species in the central basin pollen assemblage suggests it is widely dispersed or re-worked by wind and water.

Patterns across transects

Trends in the relative abundance of pollen across the different estuarine environments are best illustrated by Transect C, incorporating Sites T5-Hb, C18, C17, C16, and C-Sa (Fig 5). These sites respectively occur in the western saltmarsh, sub-aquatic western platform, central basin, sub-aquatic eastern platform, and eastern saltmarsh environments. Chenopodiaceae pollen dominate the western saltmarsh environment, decrease in abundance towards the central basin, increase again on the eastern platform, and become dominant again on the eastern saltmarsh. Gramineae pollen, away from the saltmarsh environments where they are overshadowed by the over-representation of Chenopodiaceae pollen, show a fairly consistent relative abundance across the estuary. Casuarinaceae, Restionaceae, *Olearia axillaris* and *Lepidosperma* pollen are most abundant in the central basin and decrease in abundance towards the eastern and western shores. This pattern may signal transport and deposition by currents as well as wind. Pollen of the Myrtaceae are relatively consistent across the basin, being similarly prominent on the eastern and western platforms; their lower relative abundance in the saltmarsh is likely related to the over-representation of Chenopodiaceae pollen.

In Transect B, which incorporates Sites B13, B11 and B9 (Fig 5), some species/groups have a similar pattern of distribution as in Transect C (Fig 5), whereas others are quite different. From west to east, Chenopodiaceae pollen are slightly more abundant on the platforms than in the central basin, reflecting proximity of the platforms to adjoining saltmarsh environments. Gramineae pollen is relatively consistent across the estuary, and Casuarinaceae pollen is slightly more abundant in the central basin compared to the sub-aquatic platforms, suggesting transport and deposition by currents as well as wind. *Olearia axillaris* and *Lepidosperma gladiatum* pollen show comparable trends - they are more abundant in the western platform sites close to their source, and decrease in abundance from west to east. The pollen of Myrtaceae show a trend of decreasing abundance from east to west across the estuary.

Patterns of distribution

From the transects, consistent patterns of pollen distribution can be seen for the major plant groups discussed above. Chenopodiaceae pollen decreases in abundance away from its source; Gramineae is fairly consistent across the estuary, suggesting its occurrence is relatively uniform in the surrounding vegetation; and Casuarinaceae pollen is more abundant in the central basin, possibly due to a combination of local input, currents, and long-distance aerial and fluvial delivery. Other taxa that provide insights into dispersion of pollen within the estuary are *Acacia cyclops, Eucalyptus* spp and the *Melaleuca/Agonis* group, *Lepidosperma gladiatum, Olearia axillaris,* and *Pinus.*

Acacia cyclops is restricted to specific habitats on the dune barrier. Its pollen only occurs in very low numbers adjoining its source. *Acacia* produces relatively large heavy pollen that is rarely transported far from its source. While the pollen counts presented in Table 4 refer to generalised Myrtaceae pollen (see Methods), differentiation between the pollen of *Eucalyptus* spp and the *Melaleuca/Agonis* group was attempted. The results of pollen counts show that along Transect B the pollen record is dominated by *Melaleuca/Agonis*, indicating probable derivation from *Melaleuca rhaphiophylla* wetland forests and *Agonis* scrub from the western and eastern shores; *Eucalyptus* pollen along this transect is most prominent in the central and eastern platform sites, indicating that its source is the *Eucalyptus* species (*E. gomphocephala, E. rudis, E. calophylla, E. marginata*) that inhabit the eastern shore. The shore and barrier to the west of Transect B is not dominated by *Eucalyptus* vegetation. In Transect C, *Eucalyptus* pollen is more prominent on the platforms and *Melaleuca/Agonis* dominates the central basin. *Eucalyptus* woodland occurs on the western barrier, and in the east, *Melaleuca rhaphiophylla* wetland forests, *Agonis* scrub, and the *Eucalyptus* species noted above, occur.

The patterns for *Lepidosperma gladiatum* and *Olearia axillaris* are similarly variable. Near Transect B, these species occur on both sides of the basin, but are most common on the dune barrier adjoining the western platform. Although pollen numbers are low for these species, their relative abundance across Transect B does reflect the distribution of the parent plants. Along Transect C, pollen of both species is most abundant in the central basin, indicating a possible high aerial delivery that by-passes the western platform, or a water current delivery from southern areas of the barrier dune.

Pollen of *Pinus* is ubiquitously present in low to moderate abundance (<1-12%) in most of the estuary environments. Pine plantations occur both locally and distally to the north-east of the Leschenault Inlet estuary, but there appears to be no pattern of pollen dispersal across the estuary with respect to source and wind patterns. Of interest are two samples with a particularly high pine pollen occurrence. Site A4, which contains 28% pine pollen, is the most southerly of the sub-aquatic western platform samples and the most distant from the forest source. However, this site is opposite the Collie River delta, suggesting fluvial delivery of pine pollen that has been transported to the Collie River drainage basin via wind and run-off. The most abundant occurrence of pine pollen is in a mangrove zone (Site LI-4B) where it comprises almost 55% of the pollen count. A replicate sample collected a metre away (Site 98-dune surface), and adjoining and more open saltmarsh environments (Sites LI-5B and T5-Hb), contain less than 5% pine pollen. The high relative abundance of pine pollen at Site LI-4B is inexplicable at this stage, and illustrates

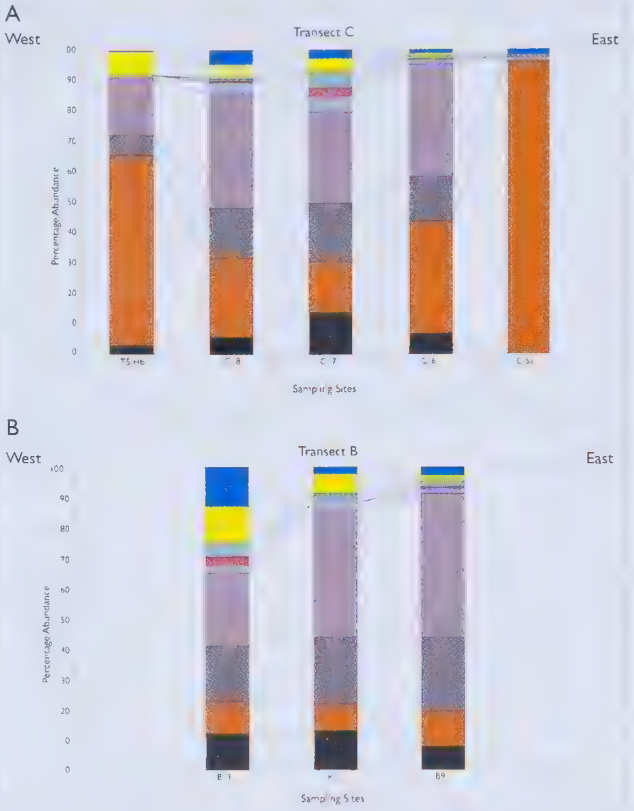

Figure 5. Occurrence of pollen of selected species/group from the contemporary surface along the east-west transects *viz* Transects B and C. Pine pollen has been excluded.

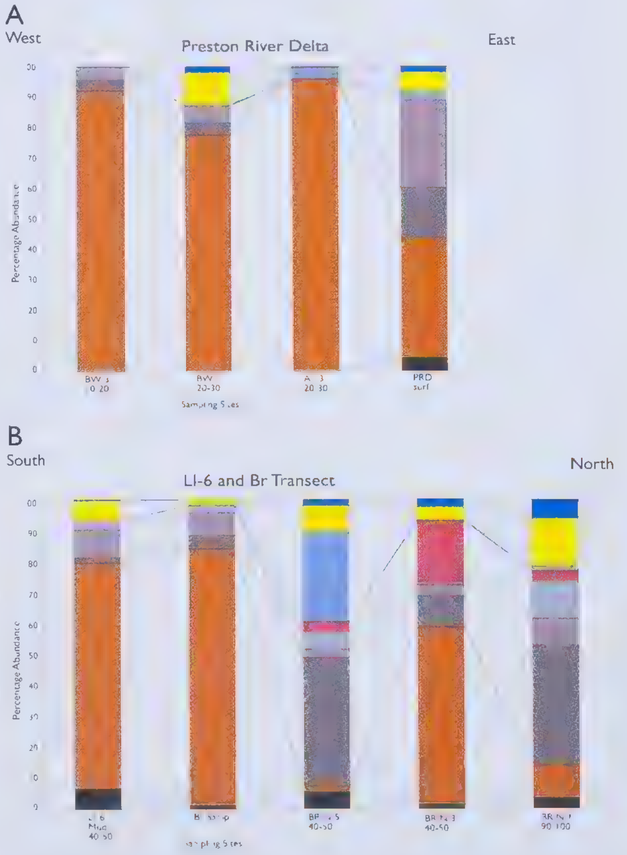

Figure 6. Comparison of occurrence of pollen of selected species/groups in the modern and sub-recent for the Preston River Delta transect and the LI-6 and BR/N transects. Pine pollen has been excluded.

well the problems posed by local over-representation of regional pollen when interpreting fossil pollen assemblages from single boreholes.

Stratigraphic results

Preston River delta (Fig 6). In the Preston River delta the contemporary sample (98 PRD surface) contains a variety of pollen types, including, in order of abundance, Chenopodiaceae (near 40%), Myrtaceae (near 30%), Gramineae, Casuarinaceae, *Pinus*, and *Frankenia pauciflora*. The three sub-recent samples (AI/3, BW/1, BW/3) are generally similar to each other in composition, but differ from the contemporary sample in being dominated by Chenopodiaceae (80-90%), with Myrtaceae and Gramineae together totalling about 10%; pollen of *Pinus* and Casuarinaceae are not present.

Northern estuary (Fig 6). In the north-eastern estuary the contemporary saltmarsh sample (Site Br-Sa) is dominated by Chenopodiaceae, with a < 20% aggregate of Myrtaceae, Gramineae, Restionaceae, *Olearia* and *Pinus*. The stratigraphic samples (Sites BR/N-1, BR/N-3, BR/N-5, and LI-6) are variable, but differ from the contemporary sample in containing markedly less Chenopodiaceae, comparatively common to abundant *Lepidosperma gladiatum*, and consistent Casuarinaceae pollen.. Locally, they contain a higher percentage of Gramineae pollen, and Myrtaceae and Restionaceae pollen are more abundant in two of the samples.

Stratigraphically, the BR/N series of samples are located in the southern 1 km part of a former muddy tidal flat to shallow water mud basin setting that prograded some 4 km in the last *ca* 3 000 years (see Semeniuk 1985 and 1995a for radiocarbon dates in this region with respect to the sea level history and the evolution of Leschenault Inlet). This places the samples collected within a time frame of the last 1 000 years.

Mangrove pollen distribution

The results of the analyses of a wide range of surface contemporary samples showed that while *Avicennia marina* pollen occurred in the samples collected from environments under mangrove canopy and in immediately adjacent environments (*e.g.* nearby non-mangrove inhabited tidal flat saltmarsh environments), it was not recorded from most estuarine surfaces (see Table 3). Significantly, *Avicennia marina* pollen was not recorded from the sub-recent samples.

Discussion

A major objective of this study was to determine if pollen assemblages could be related to depositional environment, and therefore of use in interpreting earlier Holocene sequences in the area. The results to date suggest that this is possible. The baseline studies of the contemporary sediments show that it is possible to separate the saltmarsh, western platform, central basin, and eastern platform pollen assemblages at a gross scale using family groupings, and in some instances at the generic or species level. The saltmarsh environment, dominated by Chenopodiaceae pollen, is relatively simple to differentiate. Similarly, species that are proximal to their source generate pollen abundance gradients which serve to distinguish specific environments and indicate the nature of the immediate upland source vegetation. For some sites, potential transport systems assist in explaining the distribution of palynomorphs.

Although a clearer picture of the characteristics of pollen assemblages from each environment will emerge during future studies, it is possible from the preliminary baselines to suggest the environments of deposition for some of the sub-recent samples in the northern estuary (*i.e.* BR/N series of samples). For example, the pollen assemblage from the LI-6 (40-50 cm) sample is similar to those in the contemporary saltmarsh samples (*e.g.* Br-Sa, LI-5B). In BR/N-5 (40-50 cm) and BR/N-1 (90-100 cm) the most indicative characteristic of the pollen assemblages is the relative prominence of *Lepidosperma gladiatum* and the presence of *Olearia axillaris*, together with a moderate abundance of Chenopodiaceae pollen. The most similar contemporary assemblages are in C17 from the northern central basin, and C13 on the western platform. In C17, it is thought the relative abundance of pollen of these species is due to water current or aerial transport, whereas in C13, *L. gladiatum* and *O. axillaris* are common in the adjacent vegetation. Considering the stratigraphic and prograding setting of the two BR/N samples, they may both have been deposited in a northerly section of the northern subtidal flat.

It is stressed that the results and conclusions of this study are preliminary in nature. To obtain a fuller understanding of the distribution and internal variability in the environment-related pollen assemblages, more samples across the estuary are needed, and more replication within sites and replication between sites within the same depositional unit are required.

Interpretations of the Holocene pollen record in terms of depositional environments, proximal vegetation associations, and climate change need to be based firmly on an holistic understanding of the dynamics of pollen in the modern environment. Holistic studies integrating aspects such as vegetation sources, wind patterns, depositional processes, and pollen taphonomy amongst others, are difficult and seldom attempted. To date, the emphasis in Australia has been on interpreting the pollen record in a single borehole (*e.g.* Churchill 1959, 1968; Newsome & Pickett 1993; Jenkins & Kershaw 1997; Lloyd & Kershaw 1997). While these studies are useful generally in illustrating changes in the pollen record, and are used to infer climatic and environmental changes, they are not placed in a comparative contemporary setting, nor do they offer the details of processes that may provide an explanation of the natural variability in the record to separate serial vegetation changes from that induced by local environmental changes (*e.g.* water table changes), or those actually related to climate changes. Luly (1997), however, provides a more holistic study of pollen in a playa in semi-arid Victoria, recognising that the pollen assemblages in sites of sedimentary accumulations are the result of what the author terms a "myriad of influences". From a grid of surface sampling sites, the concentration of different pollen taxa was mapped, and from pollen traps, the pollen transport pathways were characterised. The results were used in the analysis of the pollen record of two cores. Studies such as Luly's (1997), and that of the contemporary deposits of Leschenault Inlet, provide insights into the significance of pollen assemblages in a given environment, and highlight inherent problems of interpreting the pollen record from single cores without addressing the complexities of pollen dynamics.

The second objective of the Leschenault Inlet study was to determine if the mangrove *Avicennia marina* was present in the area in the recent past. *Avicennia marina* was not recorded from the sub-recent samples, either indicating that mangrove stands were too distant from the site of accumulating sediment where our samples are located, or that mangroves were in fact absent from the estuary at that time. While mangroves are present in sufficient numbers in Leschenault Inlet today to develop closed low forests and scrub, their pollen only occurs in small numbers in adjacent saltmarsh environments (*e.g.* T5-Hb, 98 PRD surface) and the northern part of the central basin (C17). The sub-recent stratigraphic samples were drawn from former tidal flat settings, targeting the zone of most likely occurrence of mangrove pollen. The previously noted similarity of the sub-recent pollen assemblages to those of the saltmarsh environment and the northern central basin (C17), both of which contain *A. marina* pollen, and the presence of *A. marina* pollen in contemporary samples from saltmarsh and proximal environments (see Table 3), confirms that the correct zone was targeted. The absence of *A. marina* pollen in the stratigraphic samples therefore suggests that mangroves were not present in the vegetation of sub-recent tidal environments of Leschenault Inlet.

Our results suggest the Leschenault Inlet mangroves are not relicts. Semeniuk *et al.* (2000) argue that *Avicennia marina* is probably a very recent arrival to the region following a change in climate linked to the effects of Earth-axis precession. The hypothesis is forwarded that during the past 7 000 years, as the Tropic of Capricorn migrated northwards, the zone of maximum aridity in Western Australia moved northwards from Shark Bay to Exmouth (Semeniuk 1995b), and the shallow waters of the Northwest Shelf, subject to a progressively more tropical arid climate, became warmer. This contributed to the Leeuwin Current, which then delivered propagules of *A. marina* southwards to the Bunbury region from the Gascoyne-Shark Bay region, a process which appears counter-intuitive to the northwards migration of the tropical zones. The mangrove populations were sustained in the Bunbury region (specifically at Leschenualt Inlet) by the quasi-tropical marine conditions that exist in the Geographe Bay to Bunbury area, where the Leeuwin Current impinges onto, and eddies northward along, the coast. To fully test this hypothesis, more intensive sampling of Holocene estuarine tidal flat sediments in the Leschenault Inlet system needs to be undertaken.

From a geoheritage perspective, the Leschenault Inlet estuary probably ranks as significant at a national level. Because of its uncomplicated north-south oriented sedimentary environments and parallel landform and vegetation units, it also provides a classic environment in which to study the dynamics of pollen deposition. In a broad sense it is a relatively simple estuarine system, yet within it is a complex of vegetation units related to landforms, and sedimentary environments influenced by fluvial input, tidal induced currents, and variable wind directions, all of which have the potential to effect pollen transport within the system. An understanding of the variability of the pollen assemblages in contemporary samples, and the processes that contribute to their composition in a given environment, will lead to a better understanding of the significance of pollen assemblages in the Quaternary record. In essence, this study has set the framework for future work and provided preliminary results to illustrate the research potential of the study area.

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Macrophyte abundance and distribution in Leschenault Inlet, an estuarine system in south-western Australia

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Abstract

The aquatic flora of Leschenault Inlet is similar to that in other southern estuaries, except that Leschenault Inlet has a relatively high diversity of red algae, and *Hormophysa triquetra* is the dominant brown alga. Total plant biomass was generally 3 000-5 000 t dry weight, with a maximum in spring. There were large differences in the biomass of seagrass and macroalgae between individual surveys, but in general seagrass biomass and total macroalgal biomass appear relatively stable in the long term. Total plant biomass per unit area in Leschenault Inlet was similar to that in the Peel-Harvey estuarine system. The major difference was the relative proportions of total biomass accounted for by seagrass, brown algae and green algae. Macrophyte biomass in Peel-Harvey is dominated by green algae, whereas in Leschenault Inlet seagrass and brown algae are dominant. The inlet appears to have been in an acceptable state under the nutrient loading regime and hydrodynamic conditions of the years when the surveys were carried out.

Keywords: Leschenault Inlet, south-western Australia, estuary, aquatic vegetation, macrophytes, *Halophila ovalis*, *Hormophysa triquetra*, macrophyte biomass

Introduction

Leschenault Inlet is the largest (*ca* 27 km²) inland waterway in the Bunbury region, and of considerable importance for recreation, fishing (commercial and amateur) and conservation. It is a long, shallow (up to 2 m deep) coastal lagoon in an interdunal depression, with shallow platforms of sand and muddy sand along the eastern side, and deep mud on the western side.

The inlet is connected to the ocean by an artificial channel ('The Cut', Fig 1), and both the Collie and Preston Rivers discharge into the inlet west and south, opposite the Cut. The construction of Wellington Dam on the Collie River has significantly reduced the volume of fresh water entering the inlet (Anon 1983) and salinities in the inlet are essentially marine for most of the year, although the northern end (north of Waterloo Head, Fig 1) becomes hypersaline in summer. Until recently the inlet was traversed by a wastewater pipeline (SCM Chemicals Ltd), carried across the estuary for part of the way by a 900 m length of rock causeway, and across the remainder by a trestle bridge. Between July and December 1992 the trestle bridge was completely removed, and a 100 m section of the (eastern) shore end of the causeway plus two smaller sections (total length 13 m), were replaced by trestle walk-ways.

The inlet is subject to the impacts of residential, industrial, agricultural and port development, and considerable recreational use. At present it is in a relatively acceptable condition, but nutrient input due to runoff from agricultural land in the catchment has the potential to create algal problems similar to those experienced in the Peel-Harvey estuarine system (Lavery *et al.* 1995). Like the Peel-Harvey, the catchment of Leschenault Inlet is largely comprised of nutrient-poor sandy soils, and there are significant ferti-

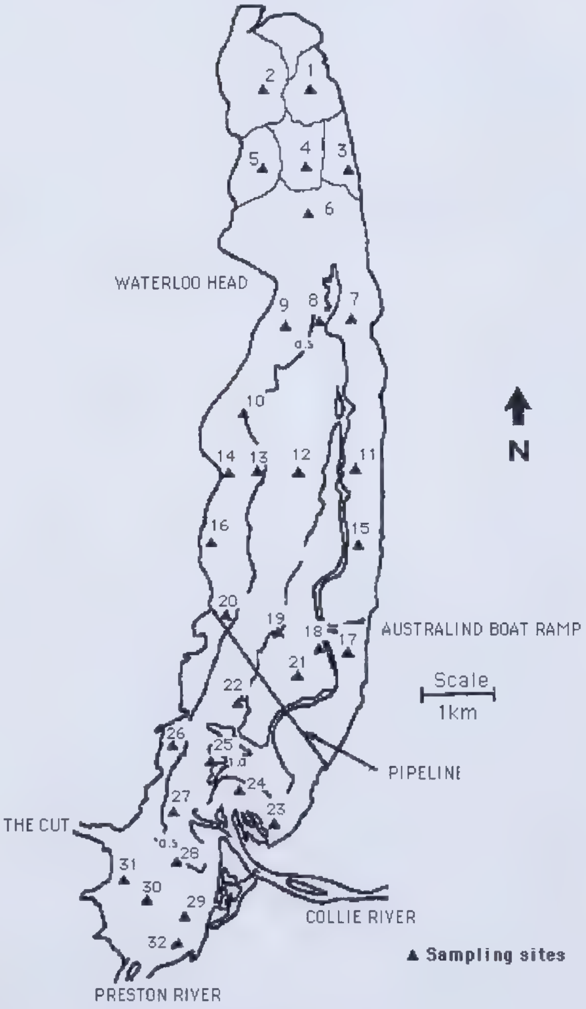


Figure 1. Leschenault Inlet, showing 0.5 and 1.0 m depth contours and sampling sites for macrophyte biomass.

Table 1. Aquatic angiosperms and macroalgae observed in Leschenault Inlet and their presence (+) or absence (-) in other south-western Australian estuaries.

	Leschenault Inlet	Peel-Harvey[*1] Estuaries	Wilson[*2] Inlet	Oyster[*3] Harbour
AQUATIC ANGIOSPERMS				
Halophila ovalis	+	+	-	+
Ruppia megacarpa	+	+	+	-
Heterozostera sp	+	-	-	+
Zostera muelleri	+	+	-	-
MACROALGAE				
CHLOROPHYTA				
Chaetomorpha linum	+	+	+	+
Lamprothamnium papulosum	+	+	+	-
Enteromorpha sp	+	+	+	+
Cladophora sp	+	+	+	-
Caulerpa sp	+	+	-	+
PHAEOPHYTA				
Hormophysa triquetra	+	-	-	-
Dictyota paniculata	+	-	+	+
RHODOPHYTA				
Gracilaria sp	+	+	+	+
Chondria sp	+	+	+	+
Laurencia sp	+	+	-	+
Spyridia filamentosa	+	-	-	+
Ceramium sp	+	*	+	+
Hypnea episcopalis	+	-	-	-

[1] Lukatelich (unpublished) (BP Refinery, Kwinana)
[2] Lukatelich *et al.*(1984)
[3] Bastyan (unpublished observations; School of Environmental Science, Murdoch University, Perth)

Table 2. The mean areal biomass in g dry wt m^{-2} for SYMAP estimates of macrophytes for Leschenault Inlet and Peel Inlet over the sampling period November 1984 to April 1993. Standard errors are generally 15-40 % of the mean.

Date	Leschenault Inlet			Peel Inlet		
	Seagrass	Macroalgae	Total macrophytes	Seagrass	Macroalgae	Total macrophytes
Nov 1984	44.7	136.0	180.7	23.8	155.8	179.6
Apr 1985	37.0	92.6	129.6	2.3	222.0	224.3
Aug 1985	21.3	46.4	67.7	5.6	207.1	212.7
Nov 1985	14.0	94.3	108.3	16.7	45.2	61.9
Oct 1987	40.7	149.9	190.6	18.2	193.4	211.6
Feb 1988	61.7	77.8	139.5	19.6	92.7	112.3
May 1988	76.2	46.8	123.0	20.2	114.3	134.5
Nov 1988	61.1	93.8	154.9	19.9	25.0	44.9
May 1989	48.8	101.2	150.0	15.5	111.5	127.0
Nov 1989	51.8	101.7	153.5	24.6	116.6	141.2
May 1990	72.1	140.3	212.4	17.5	73.4	90.9
Oct 1990	49.1	209.0	258.1	54.7	176.6	231.3
May 1991	67.9	55.7	123.6	60.1	72.2	132.3
Nov 1991	33.8	84.3	118.1	-	-	-
Mar 1992	54.1	53.5	107.6	31.7	131.7	163.4
Apr 1993	42.2	50.0	92.2	23.2	237.7	260.9

lizer inflows from agricultural areas. Leschenault Inlet receives almost the same level of nutrients as the Peel-Harvey, but lacks the associated problems of algal blooms due to a combination of effective tidal exchange and the fact that the Collie and Preston Rivers enter the inlet opposite the Cut, which ensures rapid loss of river-borne nutrients to the ocean (Anon 1990).

The present paper summarises material from a number of surveys that document seasonal and long-term variation in the spatial distribution and biomass of aquatic macrophytes in the Inlet. It incorporates data from earlier reports (Lukatelich 1985; Lukatelich 1989) and presents new data for autumn 1988 to autumn 1993. Estimates have been made of total plant biomass and individual species biomass for the dominant macrophytes, and their distributions have been mapped. Data are compared with information from other southwestern Australian estuaries.

Materials and Methods

Seasonal surveys were carried out between November 1984 and November 1985; and October 1987 and May 1988. Biannual surveys (spring and autumn) were conducted between autumn 1988 and autumn 1992, followed by one survey in autumn 1993.

Stratified macrophyte sampling was carried out at 32 sites (Fig 1) selected to best represent the environments in the Inlet. Sites were spaced at relatively regular intervals along the length of the Inlet, but across the width were selected to reflect depth intervals; fewer sites were sampled in the central basin. At each site, five replicate cores were collected by divers using Perspex corers (9 cm diameter, 50 cm long, area 64 cm^2), which were pushed into the sediment surface over the benthic macrophytes and sealed. Plant material was sieved to remove excess sediment, sorted into species categories and oven dried (70 °C) to constant weight. Dry weights were determined to two significant figures and species biomass expressed as weight per unit area. Estimates for biomass are means of five replicates. Total macrophyte biomass for an individual site was 0 to 1 000 g dry wt m^{-2}. Standard errors for the replicates from particular sites were 15-40% of the mean, the relatively high variation being accounted for by the patchy distribution of the macrophytes, though where macrophytes occurred, the cover was usually quite continuous. High variability was offset to some extent by the smoothing effect of a computer-generated mapping programme (SYMAP, Dougenik & Sheehan, 1977), which accepted data from plotted, individual sites and drew up contours of different quantities of biomass. The weights bounded by contour intervals were summed to estimate total biomass for the inlet. Before May 1989, maps were manually digitised: these were re-analyzed using SYMAP. A comparison of the manual and computer digitisation for this period revealed errors of ± 5-10 %. This is considered acceptable, but biomass data presented here for before May 1989 will differ slightly from those presented in earlier reports.

The method for estimating biomass for the entire inlet is subject to the limitations of the SYMAP method, and there were relatively few sites sampled for such a large water body, which may lead to overestimates of biomass in most cases. Nevertheless it is considered that adherence to the same sampling sites and methods over the sampling period has produced a valid representation of distribution patterns and trends over the periods investigated.

Results and Discussion

Aquatic flora

A list of species from Lukatelich (1989) is reproduced in Table 1. No further species were observed in the present study, though the list of red algae is incomplete, as there are taxonomic problems with some species. The seagrasses *Amphibolis antarctica* and *Posidonia australis* have been recorded by Anon (1983) as drift material in Vittoria Bay and around the channel entrance, but they do not appear to grow in the Inlet.

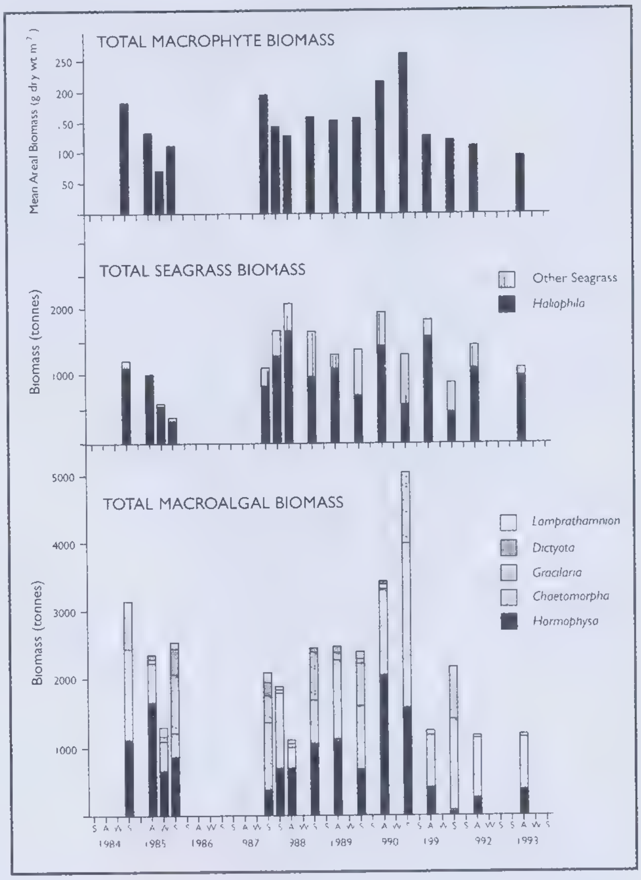
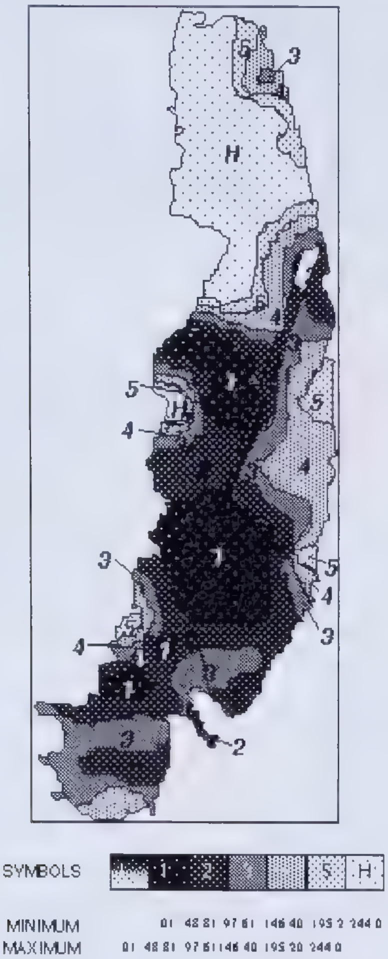


Figure 2. A: Mean areal macrophyte biomass and total biomass in Leschenault Inlet, 1984-93, in summer (S), in autumn (A), in winter (W), and in spring (S) respectively. **B:** Total seagrass biomass in Leschenault Inlet, 1984-93, in summer (S), in autumn (A), in winter (W), and in summer (S) respectively. **C:** Total biomass of major macroalgal species (tonnes) in Leschenault Inlet , 1984-93, in summer (S), in autumn (A), in winter (W), and in summer (S) respectively.

Total macrophyte biomass

Total biomass for the estuary (3 000-5 000 t dry weight) was similar on all occasions except August 1985 (1 800 t dry weight), and May and October 1990 (5 700-7 000 t dry weight respectively). Table 2 includes a breakdown into species. The value for August 1985 represents the only winter data, and low macrophyte biomass would be expected, as growth of seagrasses and macroalgae would be lowest under winter conditions of low light and temperature (Hillman *et al.* 1995; Lavery *et al.* 1995).

The high estimates (Fig 2) of macrophyte biomass per unit area in spring and autumn of 1990 are more difficult to interpret. There are few physico-chemical data for the Inlet over this period, and little evidence from rainfall data or estimates of catchment flow (Donahue & Deeley 1994) that either nutrient inputs were unusually high providing more nutrients for macrophyte growth; or that inflow was unusually low, which might have resulted in improved water clarity and more light for macrophyte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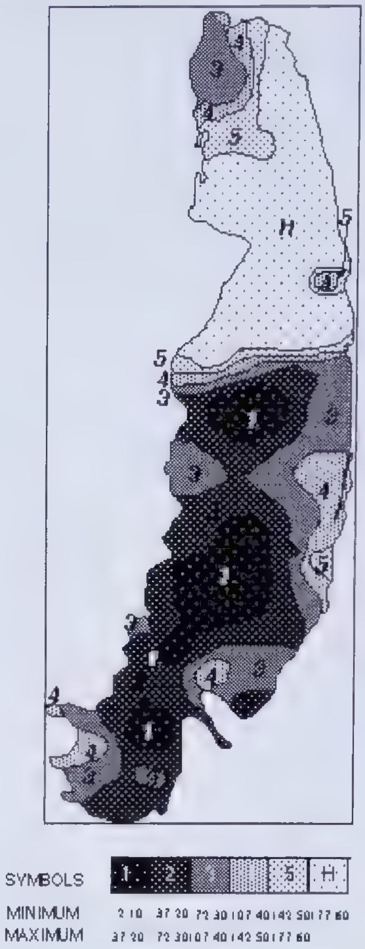
1
3
2
3
SYMBOLS
1 2 3 4 5 H
MINIMUM 01 48 81 97 61 146 40 195 2 244 0
MAXIMUM 01 48 81 97 61 146 40 195 20 244 0

Figure 4. Total macrophyte biomass for Leschenault Inlet in October 1987. Values are g dry wt m^{-2}.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SYMBOLS
1 2 3 4 5 H
MINIMUM 2 10 37 20 72 30 107 40 142 50 177 60
MAXIMUM 37 20 72 30 107 40 142 50 177 60

Figure 5. Total macrophyte biomass for Leschenault Inlet in November 1989. Values are g dry wt m^{-2}.

growth. It is likely that reduced wind stirring increased water clarity (see further discussion below) during the main macrophyte growing period (spring to autumn), but there are no data to confirm this. Given that errors for biomass estimates within a particular site were high, it is likely that apparent inconsistencies in biomass estimates for the 1990 periods (as well as spring 1984 and 1987) may well result from statistical variation.

Seasonal variation of particular macrophytes

It is possible to discern seasonal patterns for each type of macrophyte, despite the limited data set.

Seagrass. The biomass of seagrass, dominated by the species *Halophila ovalis* (Fig 2B, see Table 1 for other seagrass species present), varied from 378 t (November 1985) to 2 059 t (May 1989). The seasonal pattern of maximum biomass in late summer/early autumn and a minimum in late winter/early spring for this seagrass is similar to those reported for *Halophila* in other southwestern Australian estuaries (Hillman *et al.* 1995).

Macroalgae. Total macroalgal biomass varied from 1 261 t (May 1988) to 5 643 t (October 1990). Seasonal patterns differed for each of the algal classes comprising total macroalgal biomass. The seasonal maximum was typically reached in spring (Fig 2C), unlike the Peel-Harvey estuarine system which typically reached maximum biomass in late summer/early autumn (Lavery *et al.*1995). Red algal biomass varied from 115 t (August 1985) to 2 264 t (October 1987), with a prominent peak in spring. Spring values were 880-2 300 t, for other seasons from 100-360 t. Seasonal patterns were less clearly defined for brown and green algae. Brown algal biomass was 46 t (November 1991) to 2 069 t (May 1990). There was a general trend within each year for the seasonal maxima to be attained in autumn. Green algal biomass was 374 t (May 1988) to 2 539 t (October 1990), with no clear pattern in maximum biomass attained each year.

Comparison between Leschenault Inlet and Peel-Harvey

Total biomass. It is useful to compare estimates of total plant biomass for Leschenault Inlet with data from the Peel-Harvey. Because of the large difference in the areas of Leschenault Inlet (27 km^2) and the Peel-Harvey (total area 133 km^2; 'Peel' 84 km^2, 'Harvey' 49 km^2) the comparison must be made on an areal basis. Mean areal biomass estimates for Peel Inlet (Lavery *et al.* 1995) for the same sampling dates as Leschenault Inlet ranged from 62 to 261 g dry wt m^{-2}, with an average of 161 g dry wt m^{-2}. Mean areal biomass in Leschenault Inlet ranged from 68 to 258 g dry wt m^{-2}. (Table 3), with an average of 144 g dry wt m^{-2}. On the basis of these data, it appears that total plant biomass

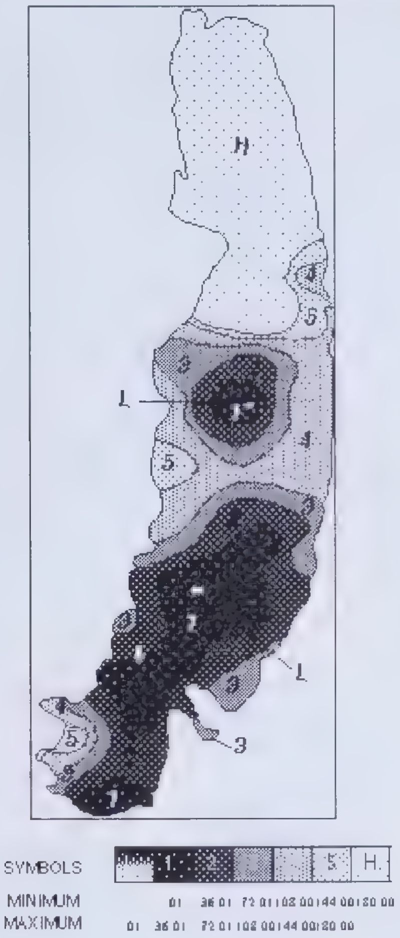

Figure 6. Total *Halophila ovalis* biomass for Leschenault Inlet in November 1991. Values are g dry wt m^{-2}.

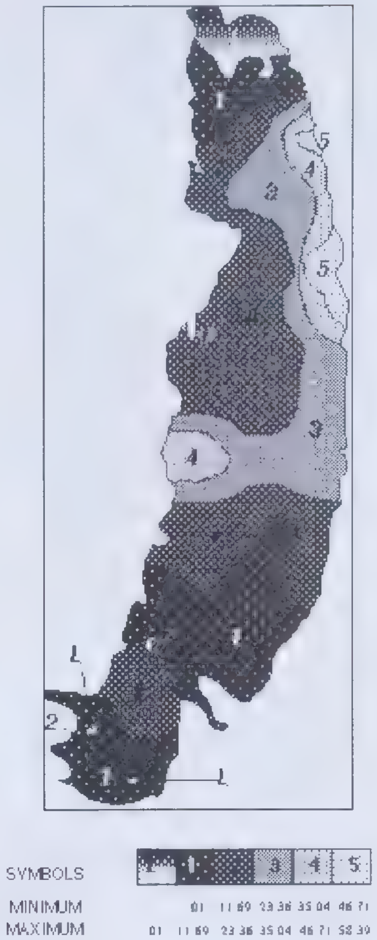

Figure 7. Total *Chaetomorpha linum* biomass for Leschenault Inlet in November 1991, mapped. Values are g dry wt m^{-2}.

per unit area is similar in the Peel-Harvey and Leschenault systems.

Biomass composition. The major difference between Leschenault Inlet and the Peel-Harvey is in the composition of the biomass. This can be summarised as follows:

1. Seagrasses accounted for > 30% of total biomass (range 12-62%) in Leschenault Inlet, whereas they account for < 15% of total biomass in the Peel-Harvey (Table 3).
2. Green algae comprised 11-43% of total plant biomass in Leschenault Inlet, whereas in the Peel-Harvey they accounted for > 85% of total macrophyte biomass.
3. Brown algae accounted for 14-49% of total macrophyte biomass in Leschenault Inlet. In contrast, in the Peel-Harvey brown algae accounted for < 0.5% of total biomass. Maximum mean areal biomass of brown algae in the Peel-Harvey is 3.7 g dry wt m^{-2}, compared with 76.6 g dry wt m^{-2} in Leschenault Inlet.
4. Red algae comprised a significant proportion (20-30%) of total biomass in Leschenault Inlet each spring, but not at other times of year (less than 10% of total biomass). In Peel Inlet red algae seldom comprised more than 10% of total macrophyte biomass at any time.

A large proportion of total macrophyte biomass in Leschenault Inlet is accounted for by seagrasses. This suggests that the overall water quality and clarity in Leschenault Inlet is better than in some other estuaries. Normally in estuaries and enclosed marine embayments with high nutrient loads, macrophytes are dominated by green algae (*e.g.* Sawyer 1965; Steffensen 1974; Buttermore 1977; Lowthion *et al.* 1985; McComb & Lukatelich 1995; Lavery *et al.* 1991).

Plant distribution and biomass

A comparison of the SYMAP distribution patterns, examples of which are given in Fig 3 to 7, indicates that on all occasions the highest plant biomass was in the northern section of the Inlet. Distribution patterns for total plant biomass appear to have changed very little (although total biomass has varied between years) since macrophyte monitoring commenced in 1984. The northern section (north of Waterloo Head, Fig 1) is very shallow (< 0.5 m) and exchange with the ocean is restricted because of its distance from the Cut, as shown by the large difference in salinities between the lower portion of the inlet and this section. The southern section of the inlet is essentially marine and was dominated by the seagrass *Halophila ovalis*. In the northern section plant biomass was dominated by the brown alga *Hormophysa triquetra*, the green alga *Chaetomorpha linum*, and the charophyte *Lamprothamnium papulosum*.

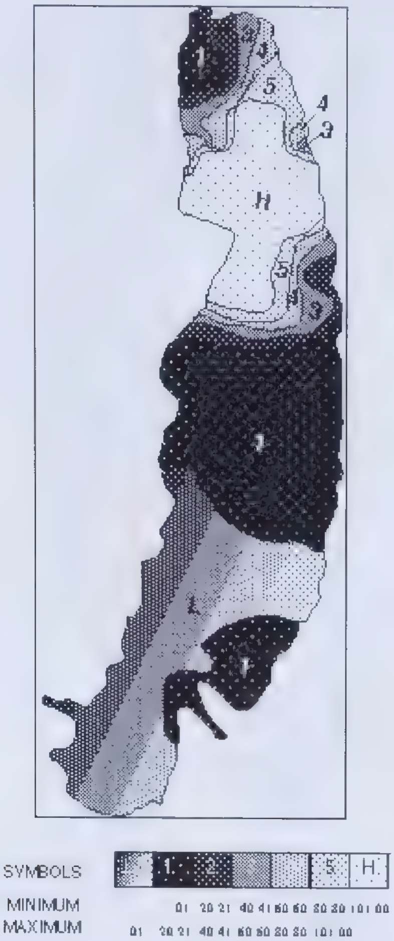

Figure 8. Total macrophyte biomass for Leschenault Inlet in November 1984. Values are g dry wt m .

As with total plant biomass, distribution patterns for individual types of macrophytes have changed little since monitoring commenced. The distribution maps depicted in Lukatelich 1989) remain valid, and have not been repeated here.

Seagrasses. *Halophila ovalis* is widely distributed in Leschenault Inlet, and is only absent from a small area of deep water in the centre of the inlet (Fig 6). Leschenault Inlet lies parallel to the prevailing southwesterly winds, and the fine, muddy sediments are easily resuspended by wind-induced mixing. This results in high turbidity, which is probably the reason for the absence of *Halophila* in the deepest sections of the inlet. Maximum areal biomass of *Halophila* was generally found just south of Waterloo Head on the sandy marginal platforms of the eastern side of the inlet. The high biomass of *Halophila* in autumn 1988), 1990 and 1991 compared to autumn 1985 may have been due to improved light penetration. *Halophila* biomass at some of the deeper sites (*e.g.* 18, 19, 22 and 25; Fig 1) was much higher in May 1988, 1990 and 1991 (see also Table 2).

Ruppia megacarpa and *Heterozostera tasmanica*, seagrasses which contribute to total seagrass biomass, were largely confined to shallower sections of the sandy marginal platform on the east of the inlet. *Zostera muelleri* was found in the inlet, but only near the entrance channel to the ocean.

Green algae. The dominant green alga in Leschenault Inlet was *Chaetomorpha linum*, which was largely confined to the northern section (Fig 7). The biomass of *Chaetomorpha* was from 298 t (May 1988) to 2 400 t (October 1990). The maximum areal biomass of this species was 705 g dry wt m^{-2} in 1990 at site 9.

The Charophyte *Lamprothamnium papulosum* was restricted to the northern section of the inlet, and attained a maximum biomass of 133 t in October 1987.

Brown algae. *Hormophysa triquetra* , the dominant brown alga, was widely distributed in the northern section of the inlet and also occurred along the eastern side as far south as the entrance to the Collie River. It had a maximum biomass of 2 030 t (May 1990) compared to 402 t (November 1985) for *Dictyota. Dictyota paniculata*, a small unattached brown alga, occurred on the eastern side of the inlet between Waterloo Head and the entrance to the Collie River. The maximum areal biomass error recorded for *Hormophysa* over the sampling period was 567 g dry wt m^{-2} in 1985 at site 2 (Table 2).

Red algae. Red algae were widespread, with a general distribution similar to that of *Halophila ovalis*. Some of the reds, in fact, occur as epiphytes on *Halophila*. The dominant red genus was *Gracilaria* and its spring biomass (the seasonal maximum) ranged from 405 t (1987) to 991 t (1990). Maximum areal biomass of *Gracilaria* was 350 g dry wt m^{-2} in 1991 at site 23 (Table 2).

Plant tissue nutrient content

There are limited data for concentrations of nitrogen and phosphorus in the tissues of macrophytes from Leschenault Inlet. Values for Ruppia and Halophila were similar, with nitrogen concentrations of 7.5-27.6 mg g^{-1} dry weight and phosphorus concentrations about one tenth of this, at 0.6-5.0 mg g^{-1} dry weight. These are within the range reported for other seagrasses (Hillman *et al.* 1995).

Tissue concentrations of the green alga *Chaetomorpha linum* were 10.1-38.8 mg N g^{-1} dry weight and 0.18-1.88 mg P g^{-1} dry weight. Such data can be most readily interpreted if they can be compared with a 'critical tissue nutrient concentration' (the concentration below which growth is limited by the nutrient concentration). If the critical concentrations determined for *Chaetomorpha linum* in Peel Inlet by Lavery *et al.* (1991) are applied, then growth of this species in Leschenault Inlet is never nitrogen limited, and only occasionally phosphorus limited, near the northern end of the inlet. These limited data imply that nutrients may not be limiting to algal growth in the Inlet. If growth is not limited by nutrient availability, an alternative hypothesis is that water clarity may be more important, at least at times, in determining macroalgal biomass, as found for the Peel-Harvey system (Birch *et al.* 1981; Gordon & McComb 1989; Lavery *et al.* 1991, 1995).

Macroalgal biomass was unusually high in spring 1990, but this did not coincide with high estimated nutrient input to the inlet (Donahue & Deeley 1994), consistent with the view that algal biomass may not be nutrient-limited.

Most seagrass and algal species found in Leschenault Inlet also occur in the Peel-Harvey, Wilson Inlet and Oyster Harbour. The well flushed and essentially marine nature of the southern section of Leschenault Inlet has resulted in a relatively low macrophyte biomass that is dominated by seagrasses. The northern section of the inlet appears poorly flushed, and has a relatively high plant biomass dominated by brown and green algae. Rooted (*Halophila* sp) and attached (*Hormophysa* sp) macrophytes dominate plant biomass, and the proliferation of free floating green algae that causes beach fouling problems in the Peel-Harvey System has not occurred. The brown alga *Hormophysa triquetra,* prominent in Leschenault, also occurs in the Swan/Canning (Allender & Smith 1978; Allender 1981) and Blackwood River estuaries; in the latter a low macroalgal species diversity compared to the Swan is attributed to the shortness of the marine phase in the Blackwood compared to the Swan, and paucity of firm substrate (Congdon & McComb 1981). Biogeographically the southwestern Australian coast has a particularly high diversity of red algae (Womersley 1981), and the largely marine nature of the southern half of Leschenault Inlet compared to estuaries which experience greater extremes of salinity, may favour the survival of these algae.

As noted above, water clarity may be a more important than nutrients in controlling plant biomass, but the data are limited. It should also be emphasised that nutrient inputs from the Parkfield Drain (which are not well documented) could be more critical than total nutrient input to the inlet. Tidal exchange and the silting of rivers probably result in a degree of 'buffering' against effects of nutrient inputs from the associated catchments, but as the magnitude of such buffering is unknown, nutrient inputs should be minimised, whilst any increase in nutrient loading to the northern section of the inlet, which is less well flushed, has the potential to result in the proliferation of nuisance green algae.

Despite high biomass in the northern section, the inlet appears to have been in an acceptable state under the nutrient loading regime and hydrodynamic conditions of the years when the surveys were carried out.

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Plankton dynamics in Leschenault Inlet and comparisons with the Peel-Harvey estuary

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Abstract

Concerns over weed accumulations on beaches and possible nutrient enrichment prompted an investigation into phytoplankton dynamics of Leschenault Inlet. The composition of the phytoplankton community, its relative density and the amplitude seasonal density changes were investigated over an eighteen month period. The zooplankton community was also sampled during summer to identify dominant organisms.

The phytoplankton community was dominated by marine and estuarine diatoms for most of the year. Species having a freshwater affinity were observed for short periods during winter, and included diatoms, dinoflagellates, cyanophytes and cryptophytes. These species were probably transported into the estuary with winter runoff from streams throughout the catchment. There was a high proportion of normally benthic or epiphytic species in surface waters consistent with very shallow depths and significant wind mixing for much of the year. Some of these species were observed attached to seagrass leaves.

There was considerable spatial and temporal variability in cell densities and species numbers throughout the estuary. Short-term blooms in excess of 5 000 cells mL^{-1} were observed in the estuary during autumn and spring. The presence of blooms indicates that Leschenault Inlet may be experiencing some nutrient enrichment although greater species numbers than observed in the highly nutrient enriched Peel and Harvey estuaries suggest that Leschenault Inlet may only be mildly nutrient enriched. Further investigations into sediment and nutrient inputs and the autecology of phytoplankton indicator species may assist in determining the nutrient status of Leschenault Inlet.

Keywords: phytoplankton, zooplankton, Leschenault Inlet, estuary, south-western Australia.

Introduction

It has been established (Kennish 1994) that estuaries are more productive than fresh water or marine ecosystems. In recent years, southwest Australian estuaries have received excessive loadings of nutrients and have displayed symptoms of increased primary productivity. Nutrient enrichment in some southwest Australian estuaries has lead to: increased phytoplankton density, mostly diatoms (John 1988), although in severe cases, potentially harmful dinoflagellates and cyanophytes have occurred (McComb & Humphries 1992; Hosja & Deeley 1993; Harris 1994); increased growth of submerged macroalgae (Gordon & McComb 1989; Lavery *et al.* 1991); and increased production of opportunistic seagrass species (Lukatelich *et al.* 1987). Excessive growth of opportunistic plant species in estuaries has also caused a loss of seagrasses (McComb & Davis 1993) through smothering by macroalgal blankets (Gordon & McComb 1989; Lavery *et al.* 1991) or through reduced light levels caused by increased epiphyte biomass (McComb & Humphries 1992).

There have been a number of investigations into the magnitude and causes of nutrient exports to southwest estuarine waters and their impact on estuarine primary production (Congdon & McComb 1980; Birch *et al.* 1986; McAlpine *et al.* 1989; Hodgkin & Hamilton 1993; Thompson & Hosja 1996) and it has been established that because of their unique characteristics, estuaries in the southwest of Western Australia are more susceptible to nutrient enrichment than those elsewhere in Australia (Deeley *et al.* 1999).

Southwestern Australian estuaries have been found to be biologically depauperate in their natural condition because of very low levels of nutrients and highly variable salinities mean that faunal assemblages in these estuaries could be expected to have a high proportion of opportunistic species (Deeley & Paling 1998). A high proportion of opportunistic species is a characteristic of anthropogenic disturbance (Warwick 1993) and it may therefore be difficult to detect the impacts of human disturbance in these systems subjected to a high level of natural disturbance (salinity changes).

Weed accumulations on beaches and a concern that nutrient enrichment was causing a decline in the ecological health of the estuary prompted an investigation into phytoplankton dynamics of Leschenault Inlet. The composition of the phytoplankton community, its relative density and the amplitude of seasonal density changes were investigated.

Materials and Methods

For phytoplankton, samples were collected from three sites in the estuary (Fig 1) at intervals of between 7 to 14 days from June 1984 to January 1986. Seagrass leaves were collected in 1998 for assessment of attached microalgae. For zooplankton, samples were collected in January 1996 at 9:00 pm.

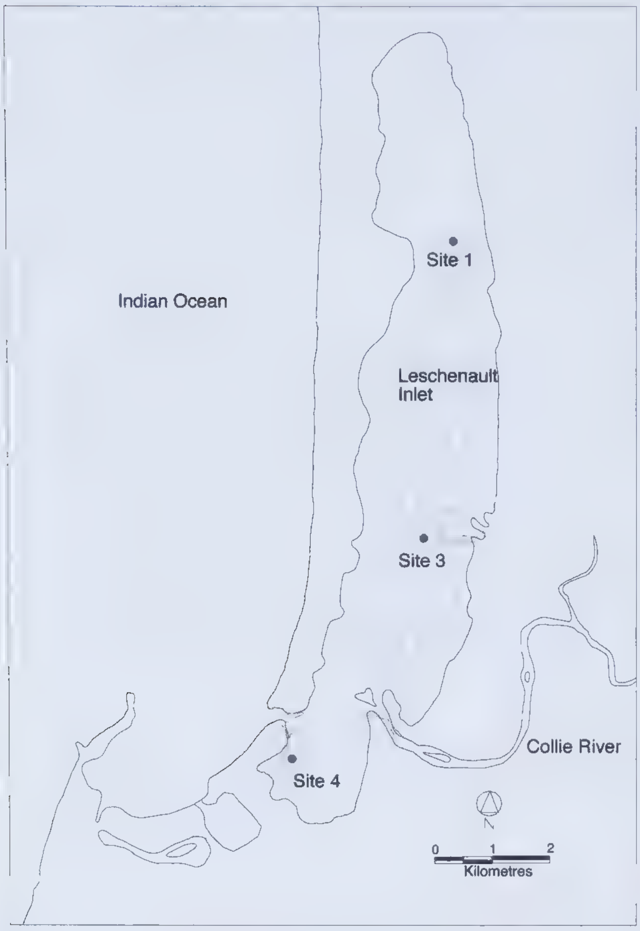

Figure 1. Location of phytoplankton sampling sites in Leschenault Inlet.

Sample collection and preservation

For phytoplankton, samples were collected between 8:30 am and 1:00 pm on all occasions. Known volumes of the surface 0.3 m of the estuary water were passed through a 5 micron net to collect phytoplankton cells. The net was rinsed and reversed at each site prior to sample collection to avoid cross contamination between sites. Samples were transferred to pre-labelled 125 ml plastic vials containing 1 ml of Lugol's iodine preservative.

To facilitate phytoplankton identification, samples of live phytoplankton were also collected at the water surface at each site and concentrated by using a phytoplankton net of 5 μm mesh pore size.

For attached phytoplankton, seagrass leaves were scraped with a razor blade and the scrapings placed into a known volume of water. Counts were then undertaken as for the phytoplankton described below. For zooplankton, vertical trawls were undertaken using a 100 μm mesh pore size (*Swiss Screens*). Samples were preserved in formalin for identification counting.

Plankton enumeration and identification

Microscopic examination of the live phytoplankton cells was carried out on the same day of collection using an Olympus BH-2 compound microscope. Some delicate species either readily rupture (*Heterosigma*) or distort (*Gyrodinium*) on preservation, requiring careful interpretation during enumeration.

Phytoplankton cell counting of the preserved cells was undertaken at 125X magnification using a 1 ml volume Sedgewick Rafter counting chamber. A correction factor was applied to allow for the dilution caused by the added preservative. Dilution or concentration techniques were applied to samples when appropriate to facilitate counting.

Some of the smallest and more delicate phytoplankton species such as the diatoms *Rhizosolenia*, *Chaetoceros* and the chrysophyte, *Pseudopedinella*, were counted using a higher magnification by leaving the coverglass off, allowing the cells to settle, and the water to partially evaporate. This permitted the observation of cells at a higher magnification (250X) by facilitating the use of the (20X) objective lens of the microscope.

Zooplankton cell counting of the preserved cells was undertaken at 125X magnification using a 1 ml volume Sedgewick Rafter counting chamber. A correction factor was applied to allow for the dilution caused by the added preservative. Dilution or concentration techniques were applied to samples when appropriate to facilitate counting.

Results

Phytoplankton species observed during summer (December–February) show that diatoms were dominant in Leschenault Inlet with lesser numbers of dinoflagellates, cyanophytes and cryptophytes (Table 1). Around 50% of species observed in the surface 0.3 m of the estuarine waters are normally considered to be benthic or epiphytic (Table 1) and this is consistent with the very shallow (mean depth 0.7 m) wind-mixed nature of the estuary.

The total number of phytoplankton cells observed at sites 1, 3 and 4 (Fig 2) show that cell densities were low at between 4 to 100 cells mL^{-1} for much of the observation period. Cell densities at all sites in winter 1984 at below 10 cells mL^{-1}, were lower than for the same sites in winter 1985 when cell densities were mostly above 10 cells mL^{-1}. There was one occasion in 1984 when cell densities at site 3 exceeded 800 cells mL^{-1}.

For 1985, cell densities were between 10 and 1 000 cells mL^{-1} for most of the year except for March and September when blooms (>1 000 cells mL^{-1}) of diatoms were observed. At site 1, cell densities during the bloom of 7th March reached 4 500 cells mL^{-1}. Cell densities at site 3 on the 7th March 1985 reached 7 000 cells mL^{-1}, and during a second bloom later in the year on the 5th September 1985 reached 10 600 cells mL^{-1}. There were periods when the cell densities at sites 1 and 3 were similar and other times when they were quite different. The blooms of the 7th March and the 5th September show that on the first occasion, sites 1 and 3 had similar cell densities while on the second occasion there was no relationship between the two sites.

The blooms observed at sites 1 and 3 were short-lived and numbers had returned to normal levels within 2 weeks of the peak densities being observed. Cell densities closest to the ocean were considerably less than those observed at the other two sites. There were no blooms observed at site 4.

The composition of phytoplankton species at site 3 (Fig

Table 1. List of phytoplankton species observed during summer (December-February).

Subclass	Order	Family	Cells mL^{-1}	Abundance[a]	Epi/Benthic[b]
Centrales	Asterolampraceae	Asterolampraceae	*Eucampia* sp 1	1	Y
Centrales	Biddulphiales	Biddulphiaceae	*Cerataulina cf pelagica*	2	N
Centrales	Coscinodiscineae	Melosiraceae	*Skeletonema costatum*	3	N
Centrales	Rhizosoleniaceae	Rhizosoleniaceae	*Rhizosolenia setigera*	3	N
Centrales	Rhizosoleniaceae	Rhizosoleniaceae	*Rhizosolenia stolterfothii*	2	N
Centrales	Rhizosoleniaceae	Rhizosoleniaceae	*Guinardia* sp 1	2	N
Centrales		Chaetoceraceae	*Chaetoceros perpusillum*	3	Y
Centrales		Chaetoceraceae	*Chaetoceros peruvianum*	1	N
Centrales		Chaetoceraceae	*Chaetoceros didymum*	3	N
Centrales		Chaetoceraceae	*Chaetoceros cf contortum*	1	N
Centrales		Chaetoceraceae	*Chaetoceros straightout*	3	N
Centrales		Chaetoceraceae	*Chaetoceros sociale/radians*	2	N
Centrales		Chaetoceraceae	*Chaetoceros* sp 3	2	N
Centrales		Chaetoceraceae	*Chaetoceros* sp 4	3	N
Centrales		Melosiraceae	*Paralia sulcata*	2	Y
Centrales		Lithodesmiaceae	*Lithodesmium undulatum*	2	N
Centrales		Heliopeltaceae	*Actinoptychus*	1	Y
Centrales		Coscinodiscaceae	*Thalassiosira* sp 1	2	N
Centrales		Coscinodiscaceae	*Thalassiosira* sp 2	2	N
Pennales	Achnanthales	Acnanthaceae	*Cocconeis* sp 1	1	Y
Pennales	Auriculaceae	Auriculaceae	*Surirella patricicae*	1	Y
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia closterium*	3	N
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia longissima*	2	Y
Pennales	Bacillariales	Nitzschiaceae	*Pseudonitzschia* sp1	2	N
Pennales	Bacillariales	Nitzschiaceae	*Pseudonitzschia* sp2	2	N
Pennales	Bacillariales	Nitzschiaceae	*Pseudonitzschia* sp3	2	N
Pennales	Bacillariales	Nitzschiaceae	*Bacillaria paxillifera*	1	Y
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia punctata*	2	Y
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia triblionella*	1	Y
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia* sp 3 vvs	2	Y
Pennales	Bacillariales	Nitzschiaceae	*Nitzschia cf linearis*	1	Y
Pennales	Fragilariales	Fragilariaceae	*Asterionellopsis glacialis*	2	N
Pennales	Fragilariales	Fragilariaceae	*Gramatophora oceanum*	2	N
Pennales	Fragilariales	Fragilariaceae	*Licmophora paradoxa*	1	Y
Pennales	Fragilariales	Fragilariaceae	*Licmophora flabellata*	1	Y
Pennales	Fragilariales	Fragilariaceae	*Licmophora lyngbyei*	1	Y
Pennales	Fragilariales	Diatomaceae	*Synedra* sp 2 med	1	Y
Pennales	Fragilariales	Diatomaceae	*Thalassionema nitzschiodes*	2	N
Pennales	Fragilariales	Diatomaceae	*Synedra*	2	-
Pennales	Fragilariales	Fragilariaceae	*Striatella unipuridata*	2	Y
Pennales	Naviculales	Cymbellaceae	*Amphora* sp1	1	Y
Pennales	Naviculales	Cymbellaceae	*Amphora hyalina*	1	Y
Pennales	Naviculales	Entomoneidaceae	*Entomoneis* sp 2	1	-
Pennales	Naviculales	Entomoneidaceae	*Entomoneis* sp 3	1	-
Pennales	Naviculales	Naviculaceae	*Mastogloia* sp 1	1	Y
Pennales			*Pennate* sp 1	2	Y
Pennales		Auriculaceae	*Surirella*	2	Y
		Leptocylindraceae	*Leptocylindrus danicus*	2	N
		Leptocylindraceae	*Leptocylindrus minimus*	1	N
	Prorocentrales	Prorocentraceae	*Prorocentrum minimum*	1	N
	Prorocentrales	Prorocentraceae	*Prorocentrum gracile*	1	N
	Dinophysales	Dinophysaceae	*Dinophysis caudata*	1	N
	Peridinales	Ceratiaceae	*Ceratium furca*	1	N
	Peridinales	Ceratiaceae	*Ceratium lineatum*	1	N
	Gymnodinales	Gymnodinaceae	*Gyrodinium spirale*	1	N
			Scrippsiella	2	N
	Peridinales	Gonyaulaceae	*Gonyaulax grindleyi*	1	N
	Peridinales	Gonyaulaceae	*Gonyaulax* sp 1	2	N
	Peridinales	Gonyaulaceae	*Alexandrium minutum*	1	N
	Peridinales	Peridinaceae	*Protoperidinium pellucidum*	2	N
	Peridinales	Peridinaceae	*Protoperidinium bipes*	2	N

Table 1 Continued. List of phytoplankton species observed during summer (December-February).

Subclass	Order	Family	Cells mL^{-1}	Abundance[a]	Epi/Benthic[b]
	Peridinales	Peridinaceae	*Protoperidinium claudicans*	2	N
	Peridinales	Peridinaceae	*Heterocapsa triquetra*	2	N
	Peridinales	Peridinaceae	*Ensiculifera*	1	N
			Katodinium	1	N
			Eutreptiella	2	N
	Cryptophyceae	Pedinales	*Apedinella*	2	N

[a] 1: Rare, 100 cells mL^{-1}; 2: Present, 100 - 1 000 cells mL^{-1}; 3: Abundant, ^{3} 1 000 cells mL^{-1}.
[b] Species normally benthic or epiphytic (Y) or not (N).

Table 2. List of species of attached microalgae observed on seagrass leaves.

Site	Abundance[a]	*Acnanthes*	*Cocconeis*	*Gramato-phora*	*Gyrosigma*	*Mastogloia* spp	*Paralia sulcata*	*Synedra* spp	Others
North of Site 4	2	3	2			3			
East of Site 3	2		1	2	2	2		3	
Site 3	2		3	3		2	2		
West of Site 3	2		1	3		2	3	3	
East of Site 1	3			1		3		3	
Site 1									
West of Site 1	2		3	2		2	3	1	

[a] 1: rare, 100 cells blade^{-1}; 2: present, 100-500 cells blade^{-1}; 3: abundant, ^{3} 500 cells blade^{-1}

3) shows that the phytoplankton community was dominated by diatoms which comprised more than 50% of the phytoplankton community from June 1984 to October 1985. From November 1985 to January 1986, dinoflagellates were dominant at more than 60% of the community. Cyanophytes and cryptophytes were most abundant during winter (April to August) and were associated with fresh water inputs from the catchment. Cryptophytes increased to 15% of the community on the 24th June 1985.

The number of phytoplankton species at each site ranged from 15 to 60 (Fig 4). Species numbers were greatest in winter and spring and reached a minimum on the 15th November 1984 and on the 16th January 1986. On most occasions, numbers of species were greatest for site 4 closest to the ocean and least at site 1 furthest from the ocean. There was a period from the 24th July 1985 until the 12th December 1985 when there were fewer species at site 3 than were observed at site 1.

Comparisons with phytoplankton communities averaged over all sites for the Peel and Harvey estuaries (Fig 5) showed on most occasions there were a greater number of species in the Leschenault Inlet than were observed in either the Peel or Harvey estuaries. The reduction in the number of species observed in Leschenault over summer

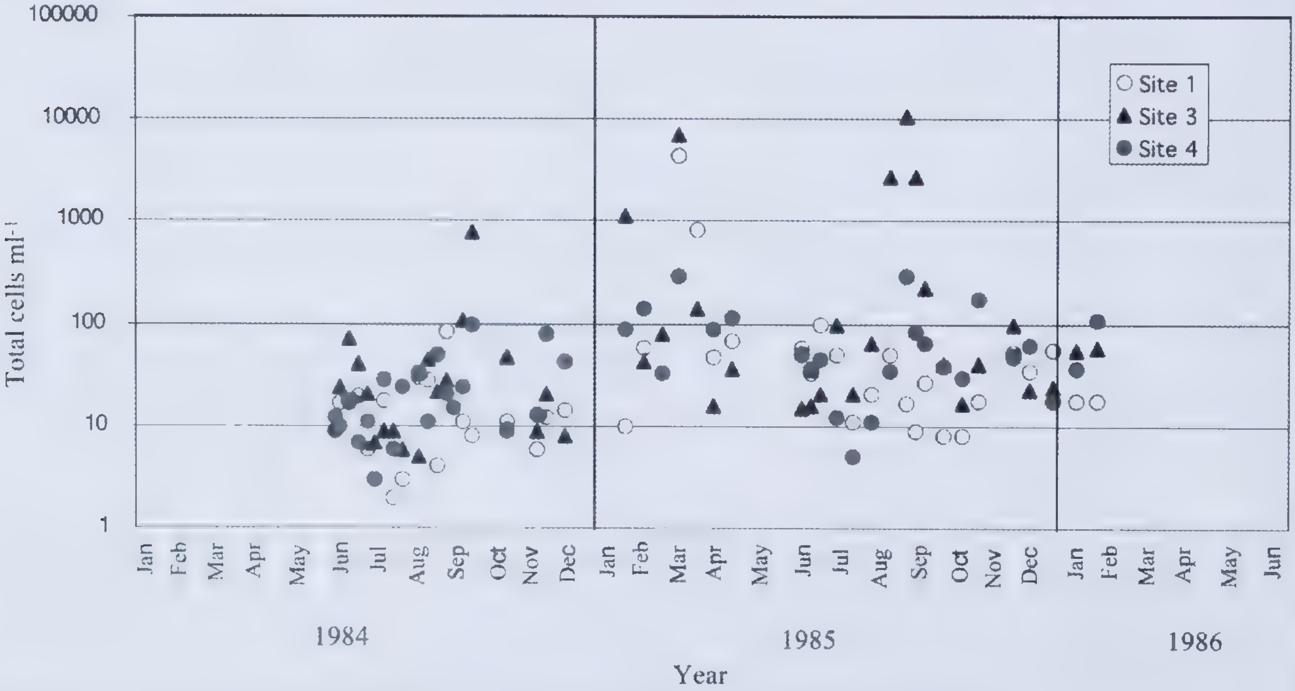

Figure 2. Cell counts for phytoplankton collected from surface water at sites 1, 3 and 4 from 1984 to 1986.

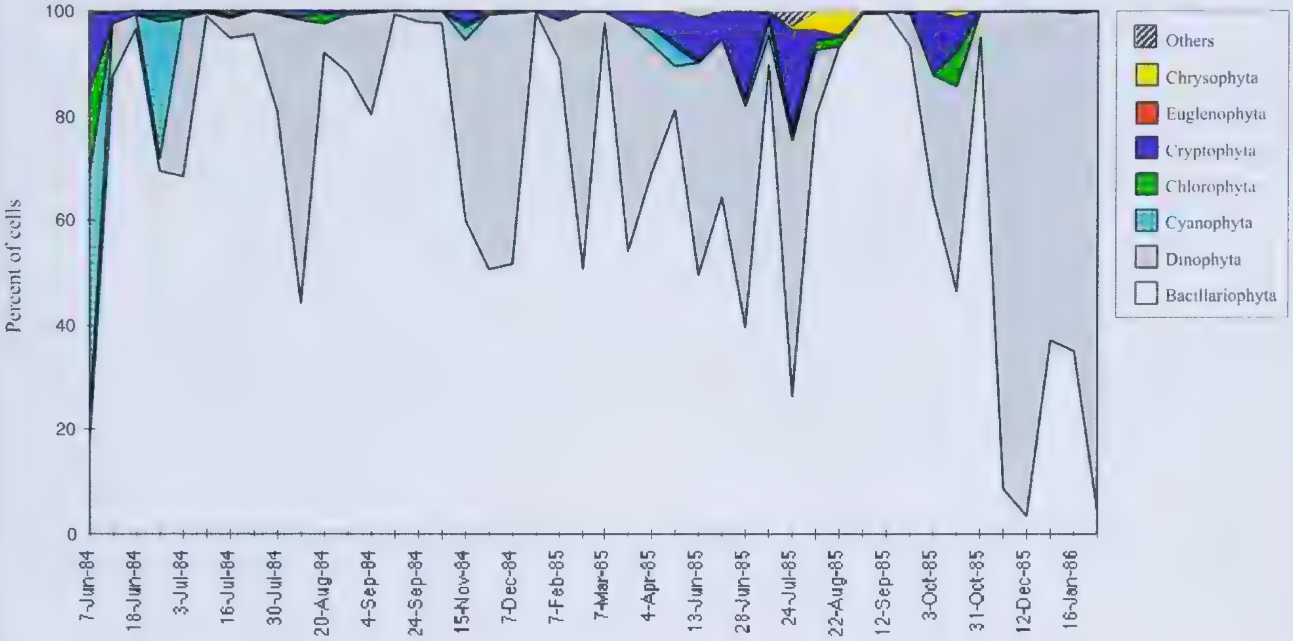

Figure 3. Composition of the phytoplankton community collected from surface water at site 3 from 1984 to 1986.

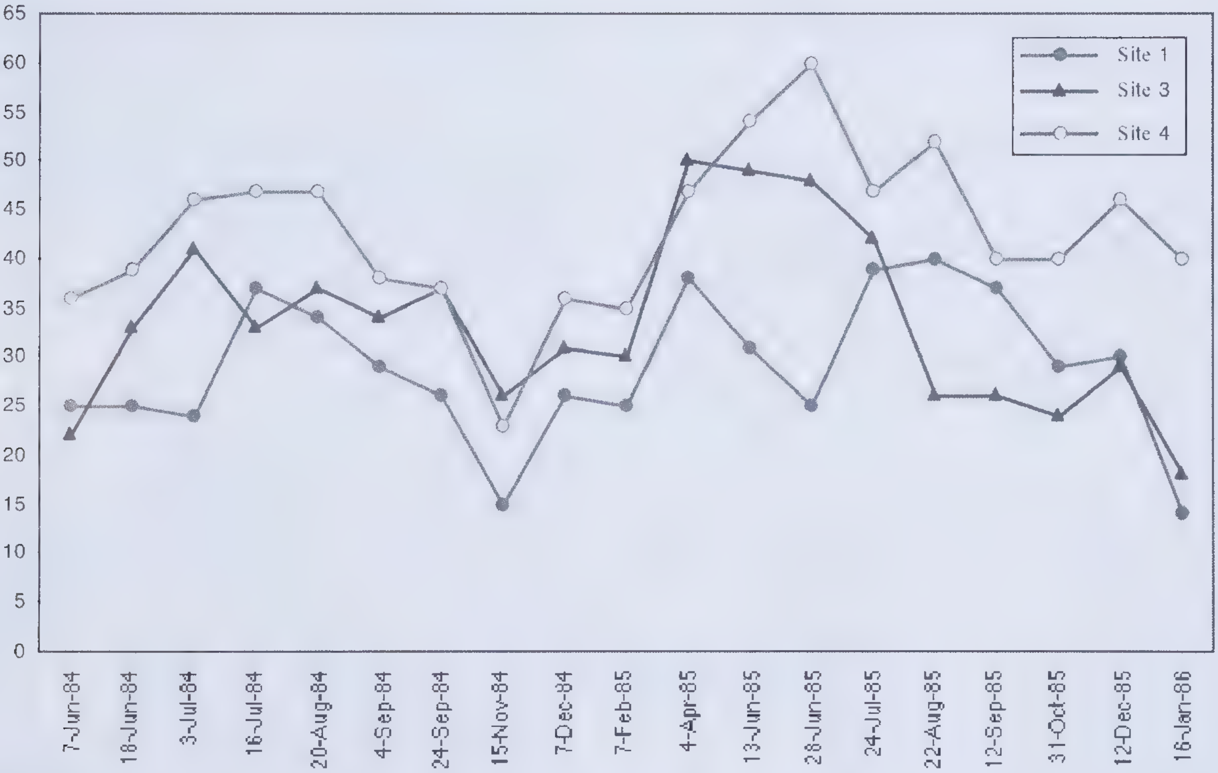

Figure 4. Number of phytoplankton species collected from surface water at sites 1, 3 and 4 from 1984 to 1986.

was also observed in the Peel and Harvey estuaries.

The attached microalgae observed on seagrass leaves (Table 2) showed similar densities to those observed in the water column (Table 1). There were many species that were identified as normally being epiphytic or benthic that were not observed on seagrass leaves. This is because benthic species which live in soft sediments would not normally be present as epiphytes on seagrasses.

Zooplankton observed in the estuarine waters during summer at night showed that 5 species were abundant having numbers in excess of 500 per vertical trawl (Table 3). There was a total of 15 zooplankton species compared to up to 60 phytoplankton species.

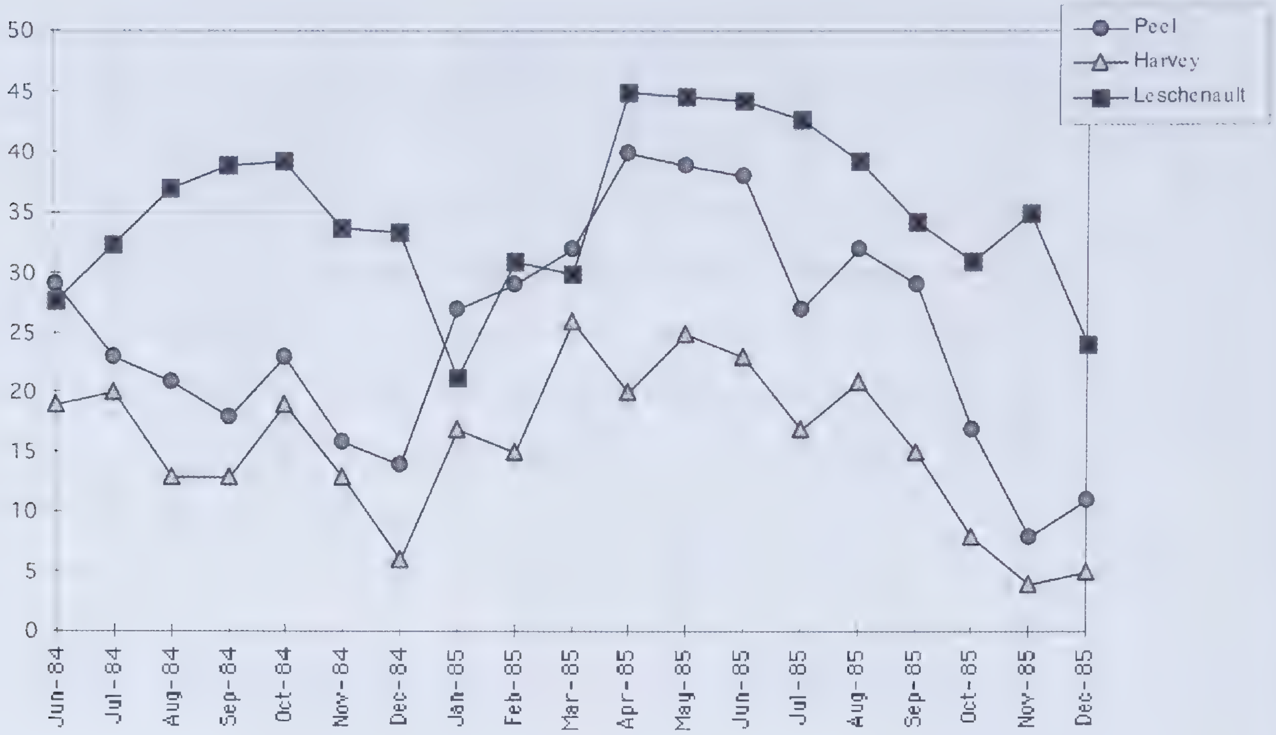

Figure 5. Average number of phytoplankton species from surface water in the Peel, Harvey and Leschenault inlets from 1984 to 1986.

Discussion

The phytoplankton community of Leschanualt Inlet was dominated by marine and estuarine diatoms for most of the year although freshwater diatoms and other groups were observed for short periods during winter. Phytoplankton species having an affinity with fresh conditions may have been transported into the estuary in winter runoff from rivers and streams further up in the catchment. Leschenault Inlet extends north south and its major axis is aligned with the prevailing southwesterly summer breezes. This means that the inlet is well-mixed for much of the year. The degree of wind mixing, together with a shallow mean depth of 0.7 m, has lead to the surface phytoplankton community containing around 50% of species normally considered to be benthic or epiphytic. These normally attached species are probably being constantly removed from substratum and entrained in the water mass where they remain for some time.

Table 3. List of zooplankton species observed during summer (December-February).

Species	Abundance[a]
Sulcanus conflictus	1
Acartiura	3
Cyclopoid sp 1	3
Cyclopoid sp 2	3
Cyclopoid sp 3	2
Copepod 1	1
Copepod 2	1
Calanoiod sp 1	2
Calanoiod sp 2	2
Hapacticoid sp 1	3
Hapacticoid sp 2	2
Hapacticoid sp 3	2
Polychaete Larvae	2
Naupius larvae	3
Malacostraca	2

[a] 1: rare, ≤ 100 cells trawl^{-1}; 2: present, 100-500 cells trawl^{-1}; 3: abundant, ^{3} 500 cells trawl^{-1}.

There were seasonal and temporal patterns in the distribution of phytoplankton species with occasional short-term blooms at some sites in excess of 5 000 cells mL^{-1}. The site closest to the ocean had the least seasonal variability in its phytoplankton community and the lowest number of species. The site most distant from the ocean had the highest number of species, and here a bloom was observed on one occasion. The site intermediate between the two had the highest cell densities, an intermediate number of species and blooms were observed on more than one occasion. These observations were consistent with a higher level of productivity in estuaries than in marine areas (Kennish 1994).

It was not possible to draw definitive conclusions as to whether the large fluctuations in cell densities at site 3 were a symptom of nutrient enrichment but blooms of this density have been associated with nutrient enrichment in other settings (Harris 1994). Comparisons with Peel and Harvey estuaries indicated that Leschenault had a higher number of species than these two estuaries that have been recognised as being highly nutrient enriched. A reduction in species richness has been associated with anthropogenic disturbance elsewhere (Patrick & Palavage 1994) and a greater number of species may indicate that Leschenault Inlet was less nutrient enriched than either Peel or Harvey estuaries.

An investigation into the autecology of particular indicator species may provide additional information on the nutrient status of Leschenault.

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Foraminifera of Leschenault Inlet

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Abstract

The foraminiferal fauna of the shallow estuarine Leschenault Inlet lagoon is very unusual. The diversity is extremely high and exceeds that encountered in the most diverse normal marine environments. Virtually all specimens recovered are devoid of protoplasm. The diversity decreases from south to north as environmental conditions change from stable normal marine to more extreme conditions.

Keywords: Leschenault Inlet, south-western Australia, estuary, foraminifera, diversity.

Introduction

The Leschenault Inlet is a shallow estuarine lagoon, separated from the Indian Ocean by the Leschenault Peninsula. The peninsula is a retrograded barrier dune system, which continues to encroach into and prograde over the estuarine environment. Semeniuk studied the physiography, sedimentology and stratigraphy of the Leschenault Inlet in a series of papers (Semeniuk 1983, 1985; Semeniuk & Meagher 1981; Wurm & Semeniuk 2000). About 40 years ago, major human intervention changed the southern part of the inlet considerably. The original outlet to the ocean was filled in, a new outlet dug out more to the north, the Preston River redirected, and an artificial canal dug.

The inlet is an elongate body of water, stretching from south to north over some 13 km, 1.5-2.5 km wide, and with a maximum depth of about 2.5 m. Contact and exchange of water with the Indian Ocean is through "The Cut", a 70 m wide and about 5 m deep channel. The Collie and Preston Rivers discharge fresh water into the southern-most part of the Inlet, while its northern-most part receives fresh water from surface run-off through the Parkfield drain. The tidal regime in the inlet is diurnal and microtidal (0.5 m on average, with a maximum range of 0.9 m), and weather conditions exert a greater influence on water levels. The inlet lies in a temperate climatic zone, with mild wet winters and hot dry summers. The average rainfall for the region is 880 mm per annum, mainly falling between April and August. Mean temperatures lie between 8 °C in winter and 28 °C in summer. Evaporation amounts to some 1980 mm per annum. In summer, winds are land breezes from the east and sea breezes from the west. In winter, winds are mainly mild easterlies, with occasional storms.

The temperature regime of the water body itself and of the sediment surface differs significantly from the land- and air-based regime. The base of the water column experiences temperatures between 10.5 °C and 33 °C. Especially the shallow and intertidal areas covered with fine, dark mud experience substantial heating effects of the sun. The water is highly oxygenated, through a combination of the shallow water column, the stirring effect of the wind and the presence of the seagrass *Halophila ovalis*. The salinity regime changes from stable, marine conditions close to "The Cut" to seasonally fluctuating conditions ranging from almost fresh water to hypersaline in the northern-most part of the inlet. On the western side of the inlet, small scale fresh water seepages result from complex interfingering of estuarine muds with sands from blown out parabolic dunes (Cresswell 2000). The sediment in the shallower peripheral parts of the inlet are sandy muds to muddy sands on the western side, and largely sands on the eastern side. The sediment in the central part of the inlet is mud.

This preliminary study documents the diversity and richness of Foraminifera found in sediments of the inlet. In the absence of any critically documented faunal studies of Foraminifera in the region, the observations cannot be put in a regional context.

Material & Methods

Sediment samples were collected on 9 May, 1999 in the Inlet at the locations shown in Fig 1. The samples are 10 cm diameter core and samples were immediately frozen upon collection. Subsequently, half of the upper 2 cm of each core was thawed (a volume of about 80 mL), washed on a 63 micron sieve and stained with Sudan Black to detect Foraminifera alive at the time of collection (Walker *et al.* 1974). Three samples came from the barrier dunes.

Foraminifera were randomly picked from the residues, mounted on faunal slides and all identified. Abundances are given in Table 1, and summaries of abundances and diversity indices are given in Table 2.

The diversity indices used are Fisher's alpha, Brillouin's H and Simpson-Yule's C. Fisher's alpha is a measure of species richness, Brillouin's H is the equivalent of the Shannon-Weaver Entropy Measure for finite populations, and Simpson's C is a measure of heterogeneity of distribution (Pielou 1977).

Ternary plots of the procentual contribution of taxa with agglutinated, porcellaneous and hyaline calcium carbonate became popular after the work of Murray (1973, 1991). Plots of this nature are shown in Fig 1 to compare and contrast the results obtained from the Foraminifera of Leschenault Inlet with those found in the literature.

Identifications

The taxonomic framework of foraminiferal classification is an increasingly fragile edifice. The scarcity of

Table 1. Abundances of foraminifera from Leschenault Inlet estuary. Sampling sites from Wurm & Semeniuk (2000). Numbers to the numbers of individuals recovered from samples. Numbers may be used as measure of relative abundance.

	Sites								
Taxon	**A4**	**B9**	**B11**	**B13**	**C16**	**C17**	**C18**	**D22**	**Total**
Ammobaculites sp	0	0	11	0	1	0	0	0	12
Ammobaculites villosus	0	0	4	0	0	0	0	0	4
Haplophragmoides sp	0	0	35	1	1	0	0	1	38
Iridia?	0	0	0	0	0	0	1	0	1
Lagenammina sp	1	0	0	0	0	0	0	0	1
Leptohalysis catena	0	0	0	1	0	0	0	0	1
Miliammina fusca	0	0	0	0	1	0	0	0	1
Nouria?	0	0	0	0	0	0	0	2	2
Paratrochammina simplissima	0	2	0	0	0	0	0	0	2
Portatrochammina sp	0	0	0	0	0	3	0	0	3
Prolixoplecta pseudofiliformis	0	1	0	0	0	0	0	0	1
Reophax sp.	0	0	3	1	0	0	0	0	4
Repmanina charoides	0	0	0	2	0	0	0	0	2
Textularia earlandi	0	0	2	0	0	1	0	0	3
Textularia lancea	0	0	1	0	0	0	0	0	1
Trochammina challengeri	0	1	63	51	0	4	18	0	137
Trochammina ochracea	2	0	0	0	0	0	0	0	2
Trochammina sp	2	0	0	0	0	0	0	0	2
Valvulina oviedoiana	0	0	2	0	0	0	0	0	2
Cornuspira involvens	2	0	0	0	0	0	0	0	2
Cornuspira planorbis	2	1	1	0	1	1	1	0	7
Dendritina striata	1	0	0	0	0	0	0	0	1
Miliolinella labiosa	0	0	0	0	0	0	0	1	1
Miliolinella subrotundata	8	0	0	0	0	0	0	0	8
Pseudolachlanella slitella	1	4	3	0	0	0	0	0	8
Quinqueloculina bicornis	0	0	0	0	8	2	0	0	10
Quinqueloculina crassicarinata	1	0	0	0	0	0	0	0	1
Quinqueloculina cuvieriana	0	0	0	2	0	0	0	0	2
Quinqueloculina eamesii	0	4	4	0	0	0	0	0	8
Quinqueloculina incisa	2	0	0	2	1	0	0	0	5
Quinqueloculina laevigata	8	0	0	0	0	22	0	0	30
Quinqueloculina patagonica	4	14	0	6	5	4	1	0	34
Quinqueloculina seminula	3	0	0	0	0	0	2	0	5
Quinqueloculina sp 1	0	2	1	2	0	0	5	0	10
Quinqueloculina sp nov	0	3	0	2	0	0	0	0	5
Quinqueloculina tenagos	0	0	0	0	1	0	0	0	1
Quinqueloculina tropicalis	1	0	0	0	0	0	0	0	1
Quinqueloculina tubicola	1	0	0	0	0	0	0	0	1
Quinqueloculina undulata	0	0	0	2	0	0	0	0	2
Sigmamiliolinella australis	4	0	0	0	0	0	0	0	4
Spiroloculina angulosa	0	3	7	2	0	0	10	0	22
Spiroloculina communis	0	0	2	1	0	0	0	0	3
Spiroloculina excisa	0	0	4	0	0	0	0	0	4
Spirophthalmidium sp	2	0	0	0	0	0	0	0	2
Triloculina australis	0	0	0	0	0	0	1	0	1
Triloculina littoralis	5	0	8	0	0	35	0	0	48
Triloculina quadrata	2	0	0	0	0	0	0	0	2
Triloculinella parisa	3	0	0	0	0	0	0	0	3
Wiesnerella auriculata	1	0	0	0	0	0	0	0	1
Conicospirillinoides inaequalis	4	0	0	0	0	0	0	0	4
Mychostomina revertens	4	0	0	0	0	0	0	0	4
Fissurina carinata	1	0	0	0	0	0	0	0	1
Fissurina lucida	2	3	1	3	0	3	1	0	13
Fissurina sp	1	1	0	0	0	0	0	0	2
Lamarckella?	0	0	2	0	0	0	0	0	2
Globigerina sp	1	0	0	0	0	0	0	0	1
Globigerinella calida	0	0	0	1	0	0	0	0	1
Abditodentrix rhomboidalis	5	0	0	0	0	0	0	0	5
Bolivina brittanica	0	0	0	0	0	1	1	0	2

Table 1 (continued). Abundances of foraminifera from Leschenault Inlet estuary. Sampling sites from Wurm & Semeniuk (2000). Numbers to the numbers of individuals recovered from samples. Numbers may be used as measure of relative abundance.

				Sites					
Taxon	**A4**	**B9**	**B11**	**B13**	**C16**	**C17**	**C18**	**D22**	**Total**
Bolivina compacta	2	0	0	0	0	0	0	0	2
Bolivina glutinata	2	1	1	2	0	0	0	0	6
Bolivina pseudoplicata	15	0	0	1	0	0	0	0	16
Bolivina striatula	7	2	7	4	0	9	0	0	29
Bolivina subreticulata	1	0	0	0	0	0	0	0	1
Bolivinella sp	1	0	0	0	0	0	0	0	1
Buliminella elegantissima	0	0	0	0	0	1	0	0	1
Cheilochanus minutus	2	0	0	0	0	0	0	0	2
Elongobula parallela	0	0	1	0	0	0	0	0	1
Globocassidulina bisecta	3	0	0	0	0	0	0	0	3
Loxostomina costatapertusa	0	0	1	0	0	0	0	0	1
Reussella aequa	0	0	0	1	0	0	0	0	1
Sagrina sp	1	2	0	0	0	0	0	0	3
Sigmavirgulina tortuosa	3	0	0	0	0	0	0	0	3
Trifarina sp	2	0	0	0	0	0	0	0	2
Ammonia tepida	32	10	75	99	8	70	76	84	454
Angulodiscorbis quadrangularis	1	0	0	0	0	0	0	0	1
Anomalinoides	5	0	0	0	0	0	0	0	5
Bronnimannia	14	0	0	0	0	0	0	0	14
Cancris carinatus	1	0	0	0	0	0	0	0	1
Challengerella bradyi	2	0	0	0	0	0	1	0	3
Cibicides mahabeti	1	0	0	0	0	1	0	0	2
Cibicides refulgens	3	0	0	0	0	0	0	0	3
Colonimilesia	2	0	0	0	0	0	0	0	2
Cymbaloporetta bradyi	1	1	0	1	0	0	0	0	3
Discorbina sp	6	0	0	0	0	0	0	0	6
Discorbinella sp 1	5	0	0	0	0	0	0	0	5
Discorbinella sp 2	2	0	0	0	0	0	0	0	2
Elphidium aculeatum	1	0	0	0	0	0	0	0	1
Elphidium advenum	7	3	0	0	0	0	0	0	10
Elphidium clavatum	11	0	7	12	2	0	8	17	57
Elphidium crispum	0	0	0	21	0	0	2	0	23
Elphidium excavatum	0	0	1	0	0	0	0	0	1
Elphidium fichtelianum	5	0	0	0	0	0	0	0	5
Elphidium jenseni	12	4	0	0	6	11	2	0	35
Elphidium lene	2	0	0	0	0	0	0	0	2
Elphidium limbatum	12	0	0	0	0	2	0	0	14
Elphidium reticulosum	0	0	0	4	0	0	11	18	33
Elphidium sp 1	10	0	2	0	1	1	0	0	14
Elphidium striatopunctatum	0	0	1	0	0	0	0	0	1
Gavelinopsis sp.	2	3	1	0	0	0	0	0	6
Glabratella sp 1	1	1	3	0	0	0	0	0	5
Glabratella sp 2	1	0	0	0	0	0	0	0	1
Glabratella sp 3	1	0	0	0	0	0	0	0	1
Milesia sp	4	0	0	0	0	0	0	0	4
Neoglabratella sp.	2	0	0	0	0	0	0	0	2
Neorotalia stellata	14	0	4	14	0	0	2	0	34
Nonion pauperatum	1	0	0	0	0	0	0	0	1
Nonion subturgidum	1	0	0	0	0	0	0	0	1
Nonionellina labradorica	0	0	1	0	0	0	0	0	1
Orbitina carinata	0	0	0	1	0	0	0	0	1
Parrellina hispidula	7	0	5	9	0	12	24	9	66
Patellina corrugata	1	0	0	0	0	0	0	0	1
Planorbulina acervalis	1	0	0	0	0	0	0	0	1
Porosononion sp 1	5	1	5	1	0	3	18	2	35
Porosononion sp 2	0	0	8	3	0	0	0	0	11
Pseudoeponides?	0	0	0	1	0	0	0	0	1
Rosalina bulloides	4	1	0	1	0	0	0	0	6
Rosalina pellucida	0	0	0	0	0	1	0	0	1
Svratkina australis	0	0	0	1	0	0	0	0	1

Table 2. Foraminiferal abundance, diversity indices, and percentage of wall structure groups at the various sampling sites.

	Sites								
	A4	**B9**	**B11**	**B13**	**C16**	**C17**	**C18**	**D22**	**Total**
No. of specimens	293	68	277	255	36	187	185	134	1435
No. of species	74	23	34	32	12	20	19	8	118
Fisher's Alpha	31.87	12.22	10.18	9.67	6.31	5.67	5.31	1.86	30.47
Brillouin's H	3.48	2.36	2.33	2.06	1.73	1.93	1.89	1.12	3.09
Simpson's C	0.03	0.08	0.15	0.20	0.13	0.20	0.21	0.43	0.12
Agglutinated	1.71%	5.88%	43.68%	21.96%	8.33%	4.28%	10.27%	2.24%	15.26%
Porcellaneous	17.41%	45.59%	10.83%	7.45%	44.44%	34.22%	10.81%	0.75%	16.17%
Hyaline	80.89%	48.53%	45.49%	70.59%	47.22%	61.50%	78.92%	97.01%	68.57%

monographic and revisional studies in general poses serious problems for routine identifications. The absence of critically documented faunal studies for the region does not alleviate the problem for the present study.

Therefore, I have reluctantly taken the more prudent approach of resorting to the use of open nomenclature. This allows the assessment of diversity and the changes in diversity within the Inlet, but it remains unsatisfactory because it does not allow comparisons with faunas elsewhere.

A number of taxa appear to be new to science. These are not included in the overall analysis and the diversities calculated are therefore somewhat lower than the actual diversity in the inlet.

Results

Foraminifera are quite rare in the dune samples, and most of them are altered. Abrasion and etching are common, and some specimens are infilled and iron-stained. Specimens washed into the sediments of the estuary are easily recognisable as allochtonous, but these are quantitatively insignificant.

The foraminiferal species spectrum of the dune sands is very different from that of the estuarine sediments. Apart from the obvious effects of winnowing and sorting, the source of foraminiferal specimens in the dune sands is the Indian Ocean.

Out of a total of 1435 specimens, only 6 were living at the time of collection. The number of species identified amounts to 118 for the estuary as a whole. Table 1 lists all the taxa and their abundance in each sample. Table 2 provides a summary by listing abundance, diversity indices and percentage of the wall structure groups. The dominant species is *Ammonia tepida*, followed by *Paratrochammina challengeri* and *Parrellina hispidula*.

Planktonic taxa are absent from the inlet. The two specimens belonging to the globigerinids have been washed in from the Indian Ocean. With the exception of a single specimen of *Planorbulina acervalis*, encrusting forms are absent as well. Examination of *Halophila ovalis* leaves revealed no epibionts except for a dense cover of diatoms. Foraminifera typically associated with the more marginal environments, such as *Ammotium salsum*, *Jadammina macrescens*, *Miliammina fusca* are essentially absent. Some of the samples yielded a number of juveniles, mainly, but not exclusively, of *Ammonia tepida*.

Discussion

The high foraminiferal diversity is unexpected and anomalous. In his compilation, Murray (1991) summarised the diversity observed in modern environments. The most diverse environments listed are Upper and Lower Slope, with a Fisher alpha index between 1 and 22 and a Shannon-Weaver H index between 0.75 and 4.1. Lagoons harbour species numbers yielding Fisher alpha indices between less than 1 to a maximum of 12. Table 2 lists, for the inlet as a whole, a Fisher alpha index of 30.37 and a Brillouin H index of 3.1. Closer inspection reveals that these numbers are due mainly to sample A4. Omitting this sample and recalculating the overall diversity yields a Fisher alpha index of 16.46, which is still very high and certainly exceeds that expected for a marine lagoonal setting.

This high foraminiferal diversity anomaly is difficult to explain. Reworking or the accumulation of foraminiferal tests over hundreds, if not thousands, of years is not an explanation. The geological history of the inlet (see Semeniuk 2000) shows that it has been a very shallow, marginal marine environment for a long time. Even if the high diversity is the result of a mix of species accumulated over this period of time, it remains unclear why so many different species found at least a temporary niche in the inlet. The pristine state of preservation of the vast majority of specimens argues against the possibility of reworking. The top 2 cm of core used represents a time slice which is to be measured in years, certainly not centuries, let alone millennia. Therefore, the diversity measured represents the actual, present diversity.

The purely benthic nature of the fauna is clearly indicative of shallow water. The absence of planktonic taxa implies no significant transport of specimens from the ocean into the inlet.

A puzzling outcome of this study is the virtual absence of specimens alive at the time of collection. The use of the Sudan Black stain is a very effective, consistent and reliable method to identify the presence of protoplasm and is unquestionably superior to the more traditional use of Rose Bengal (see Walker *et al.* 1974). The absence of stained specimens is not due to technical shortcomings. The discrepancy between the very low numbers of live specimens and the moderate to high numbers of tests in the sediments may be the result of reproductive strategies and populations dynamics. If the Foraminifera reproduce episodically, either seasonally or opportunistically, the number of tests in the sediments can thus be generated, while a single collection may easily miss the actual point in time when living organisms are present. However, this is at variance with the implications following on from the high diversity observed. From a traditional ecological perspective, a high diversity would be accompanied by at least a reasonably large standing crop. A monitoring program is the only way of resolving this issue.

The decrease in diversity along the south-north axis of Leschenault Inlet falls within expectations. The aquatic environment becomes more marginal, with the physical parameters becoming more variable and more extreme when moving from the area closest to "The Cut" to the northern-most part of the Inlet.

The limited data also show an increase in diversity along a west-east transect. This increase, observed along transects B and C, is somewhat peculiar: the total number of specimens recovered decreases, while the number of species decreases but not so fast. The Fisher alpha index therefore increases, and heterogeneity increases as well as shown by the Simpson C index (Table 2). These west-east increases coincide with an increase in the relative contri-

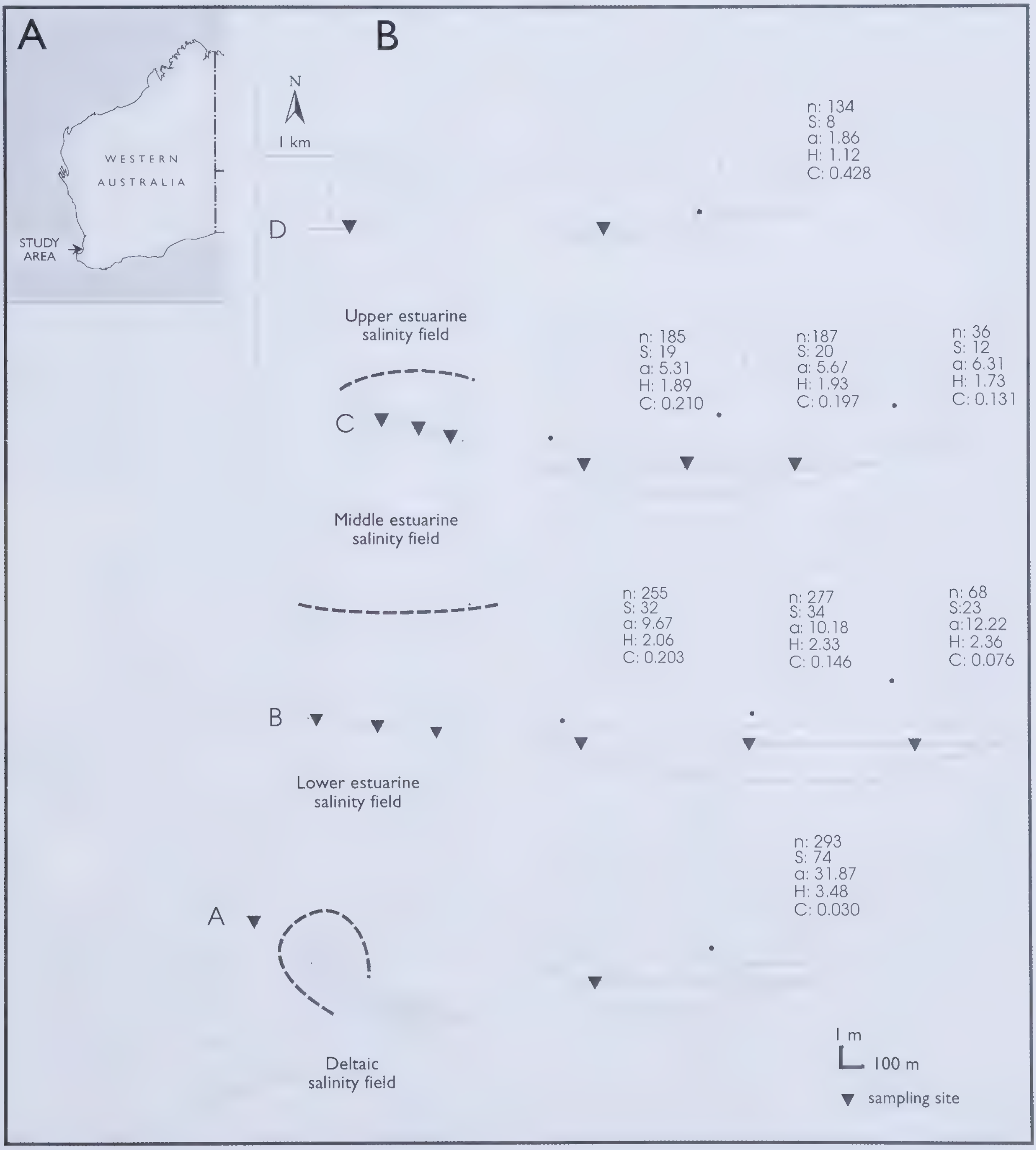

Figure 1. Sampling sites for foraminifera along transects within Leschenault Inlet. Cross sections show bathymetric profile and sampling locations. Ternary plots (after the work of Murray 1973, 1991) and information on abundance and diversity are shown for each sampling site.

bution of the porcellaneous taxa to the overall species spectrum (Fig 1). The raw data show that this increase is due to the reduction in numbers and diversity of the hyaline taxa, rather than an increase in porcellaneous taxa.

The macroscopically recognised habitats on the western margin of the inlet are substantially more diverse than on the eastern side (Wurm & Semeniuk 2000). The complex interfingering of mud-rich inlet sediments with the sands from blowouts of the parabolic dunes, combined with the resulting freshwater seeps, create a diversity of habitats which is reflected in the number of habitats on a scale relevant to the Foraminifera. The boundaries between the various macroscale habitats create micro-environments, possibly changing quite rapidly and episodically, to provide micro-organisms with a richness of niches.

From a foraminiferal point of view, the Leschenault Inlet is certainly an exceptional environment.

Acknowledgements: I thank V Semeniuk for inviting me to carry out this study, for providing the samples, and for the many useful discussions.

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Appendix

List of species of foraminifera identified in sediments from Leschenault Inlet. Species illustrated in plates 1-4. Bar scale for all foraminifera shown in the plates is 100 μm.

Agglutinating taxa

Ammobaculites sp Plate 1 Fig 1
Ammobaculites villosus Saidova 1975 Plate 1 Figs 2-3
Haplophragmoides sp Plate 1 Figs 4-5
?*Iridia* sp Plate 1 Fig 6
Lagenammina sp Plate 1 Figs 7-8
Leptohalysis catella (*Reophax catella* Höglund 1947) Plate 1 Figs 9-10
Miliammina fusca (*Quinqueloculina fusca* Brady 1870) Plate 1 Figs 11-12
?*Nouria* sp Plate 1 Figs 13-14
Paratrochammina challengeri Brönnimann & Whittaker 1988 Plate 1 Figs 15-16
Paratrochammina simplissima (*Trochammina pacifica* var *simplissima* Cushman & McCulloch 1948) Plate 1 Figs 17-18
Portatrochammina sp Plate 1 Figs 19-20
Prolixoplecta pseudofiliformis (*Gaudryina pseudofiliformis* Cushman 1911) Plate 1 Figs 21-22
Reophax sp Plate 1 Fig 23
Repmanina charoides (*Trochammina squamata* var *charoides* Jones & Parker 1860) Plate 1 Fig 24
Textularia earlandi Parker 1952 Plate 1 Figs 25-26
Textularia lancea Lalicker & McCulloch 1940 Plate 1 Figs 27-28
Trochammina ochracea (*Rotalina ochracea* Williamson 1858) Plate 1 Figs 29-30
Trochammina sp Plate 1 Figs 31-32
Valvulina oviedoiana d'Orbigny 1839 Plate 1 Fig 33

Porcellaneous taxa

Cornuspira involvens (*Operculina involvens* Reuss 1850) Plate 1 Figs 34-35
Cornuspira planorbis Schultze 1854 Plate 1 Figs 36-37
Dendritina striata Hofker 1951 Plate 1 Figs 38-39
Miliolinella labiosa (*Triloculina labiosa* d'Orbigny 1839) Plate 1 Fig 40
Miliolinella subrotunda (*Vermiculum subrotundum* Montagu 1803) Plate 1 Fig 41
Pseudolachlanella slitella Langer 1992 Plate 1 Figs 42-43
Quinqueloculina bicornis (*Serpula bicornis* Walker & Jacob 1798) Plate 1 Figs 44-45
Quinqueloculina crassicarinata Collins 1958 Plate 1 Fig 46
Quinqueloculina cuvieriana d'Orbigny 1839 Plate 1 Figs 47-78
Quinqueloculina eamesii (*Triloculina eamesii* Rasheed 1971) Plate 1 Figs 49-50
Quinqueloculina incisa Vella 1957 Plate 1 Figs 51-52
Quinqueloculina laevigata d'Orbigny 1839 Plate 1 Figs 53-54
Quinqueloculina patagonica d'Orbigny 1839 Plate 2 Figs 1-2
Quinqueloculina seminula (*Serpula seminulum* Linnaeus 1758) Plate 2 Figs 3-4
Quinqueloculina sp 1 Plate 2 Figs 5-6
Quinqueloculina sp nov Plate 2 Figs 7-8
Quinqueloculina tenagos Parker 1962 Plate 2 Figs 9-10

Quinqueloculina tropicalis Cushman 1924 Plate 2 Figs 11-12
Quinqueloculina tubicola Zheng 1979 Plate 2 Figs 13-14
Quinqueloculina undulata d'Orbigny 1852 Plate 2 Figs 15-16
Sigmamiliolinella australis Plate 2 Figs 17-18
Spiroloculina angulosa Cushman & Todd 1944 Plate 2 Figs 19-20
Spiroloculina communis Cushman & Todd 1944 Plate 2 Figs 21-22
Spiroloculina excisa (Spiroloculina communis var *excisa* Cushman & Todd 1944*)* Plate 2 Figs 23-24
Spirophthalmidium sp
Triloculina australis Parr 1932
Triloculina littoralis Collins 1958 Plate 2 Figs 25-26
Triloculina quadrata Collins 1958 Plate 2 Figs 27-28
Triloculinella parisa Loeblich & Tappan 1994 Plate 2 Figs 29-30
Wiesnerella auriculata (Planispirina auriculata Egger 1893*)* Plate 2 Fig 31

Hyaline taxa

Conicospirillinoides inaequalis (Spirillina inaequalis Brady 1879*)* Plate 2 Figs 32-33
Mychostomina revertens (Spirillina vivipara var *revertens* Rhumbler 1906*)* Plate 2 Figs 34-35
Fissurina carinata (Lagena fasciata var *carinata* Sidebottom 1906*)* Plate 2 Figs 36-37
Fissurina lucida (Entosolenia marginata var *lucida* Williamson 1848*)* Plate 2 Figs 38-39
Fissurina sp Plate 2 Figs 40-41
?Lamarckella sp
Globigerina sp Plate 2 Fig 42
Globigerinella calida (Globigerina calida Parker 1962*)* Plate 2 Fig 43
Abditodentrix rhomboidalis (Textularia rhomboidalis Millett 1899*)* Plate 2 Fig 44
Bolivina brittanica Macfadyen 1942 Plate 2 Figs 45-46
Bolivina compacta (Bolivina robusta var *compacta* Sidebottom 1905*)* Plate 2 Figs 47-48
Bolivina glutinata Egger 1893 Plate 2 Figs 49-50
Bolivina pseudoplicata Heron-Allen & Earland 1930 Plate 2 Figs 51-52
Bolivina striatula Cushman 1922 Plate 2 Figs 53-54
Bolivina subreticulata Parr 1932 Plate 3 Figs 1-2
Bolivinella barcooae (Rugobolivinella barcooae Cann & Hayward 1990*)* Plate 3 Figs 3-4
Buliminella elegantissima (Bulimina elegantissima d'Orbigny 1839*)*
Cheilochanus minutus Loeblich & Tappan 1994 Plate 3 Figs 5-6
Elongobula parallela (Buliminella parallela Cushman & Parker 1931*)* Plate 3 Fig 7
Globocassidulina bisecta Nomura 1983 Plate 3 Figs 8-9
Loxostomina costatapertusa Loeblich & Tappan 1994 Plate 3 Fig 10
Reussella aequa Cushman & McCulloch 1948 Plate 3 Figs 11-12
Sagrina sp Plate 3 Figs 13-14
Sigmavirgulina tortuosa (Bolivina tortuosa Brady 1881*)* Plate 3 Fig 15
Trifarina sp Plate 3 Figs 16-17
Ammonia tepida (Rotalia beccarii var *tepida* Cushman 1926*)* Plate 3 Figs 18-19
Angulodiscorbis quadrangularis Uchio 1953 Plate 3 Fig 20
?Anomalinoides sp Plate 3 Figs 21-22
?Bronnimannia sp Plate 3 Figs 23-24
Cancris carinatus (Pulvinulina oblonga var *carinata* Millett 1904*)* Plate 3 Figs 25-26
Challengerella bradyi Billman, Hottinger & Oesterle 1980 Plate 3 Figs 27-28
Cibicides mabahethi Said 1949 Plate 3 Figs 29-30
Cibicides refulgens Montfort 1808 Plate 3 Figs 31-32
?Colonimilesia sp Plate 3 Figs 33-34
Cymbaloporetta bradyi (Cymbalopora poeyi var *bradyi* Cushman 1915*)* Plate 3 Figs 35-36
Discorbina sp Plate 3 Figs 37-38
Discorbinella sp 1 Plate 3 Figs 39-40
Discorbinella sp 2 Plate 3 Figs 41-42
Discorbinella sp 3 Plate 3 Figs 43-44
Elphidium aculeatum (Polystomella aculeata d'Orbigny 1846*)* Plate 3 Figs 45-46
Elphidium advenum (Polystomella advena Cushman 1922*)* Plate 3 Figs 47-48
Elphidium clavatum (Elphidium incertum var *clavatum* Cushman 1930*)* Plate 3 Figs 49-50
Elphidium crispum (Nautilus crispus Linnaeus 1758*)* Plate 3 Figs 51-52
Elphidium excavatum (Polystomella excavata Terquem 1875*)* Plate 3 Figs 53-54
Elphidium fichtelianum (Polystomella fichtelianum d'Orbigny 1846*)* Plate 4 Figs 1-2
Elphidium jenseni (Polystomella jenseni Cushman 1924*)* Plate 4 Figs 3-4
Elphidium lene (Elphidium incertum var *lene* Cushman & McCulloch 1940*)* Plate 4 Figs 5-6
Elphidium limbatum (Polystomella macellum var *limbatum* Chapman 1907*)* Plate 4 Figs 7-8
Elphidium reticulosum Cushman 1933 Plate 4 Figs 9-10
Elphidium sp 1 Plate 4 Figs 11-12
Elphidium striatopunctatum (Nautilus striatopunctatus Fichtel & Moll 1798*)* Plate 4 Figs 13-14
Gavelinopsis sp Plate 4 Figs 15-16
Glabratella sp 1 Plate 4 Figs 17-18
Glabratella sp 2 Plate 4 Figs 19-20
Glabratella sp 3 Plate 4 Figs 21-22
Milesia sp Plate 4 Figs 23-24
Neoglabratella sp Plate 4 Figs 25-26
?Neorotalia stellata (Calcarina stellata de Férussac 1827*)* Plate 4 Figs 27-28
Nonion pauperatum (Nonionina pauperata Balkwill & Wright 1885*)* Plate 4 Figs 29-30
Nonion subturgidum (Nonionina subturgida Cushman 1924*)* Plate 4 Figs 31-32
Nonionellina labradorica (Nonionina labradorica Dawson 1860*)* Plate 4 Figs 33-34
Orbitina carinata Sellier de Civrieux 1977 Plate 4 Figs 35-36
Parrellina hispidula (Elphidium hispidulum Cushman 1936*)* Plate 4 Figs 37-38
Patellina corrugata Williamson 1858 Plate 4 Figs 39-40
Planorbulina acervalis Brady 1884 Plate 4 Figs 41-42
Porosononion sp 1 Plate 4 Figs 43-44
Porosononion sp 2 Plate 4 Figs 45-46
Pseudoeponides? Plate 4 Figs 47-48
Rosalina bulloides d'Orbigny 1839 Plate 4 Figs 49-50
Rosalina pellucida (Discorbis pellucidus Said 1949*)* Plate 4 Figs 51-52
Svratkina australis (Discorbis tuberculata var *australis* Chapman, Parr & Collins 1934*)* Plate 4 Figs 53-54

Plate 1

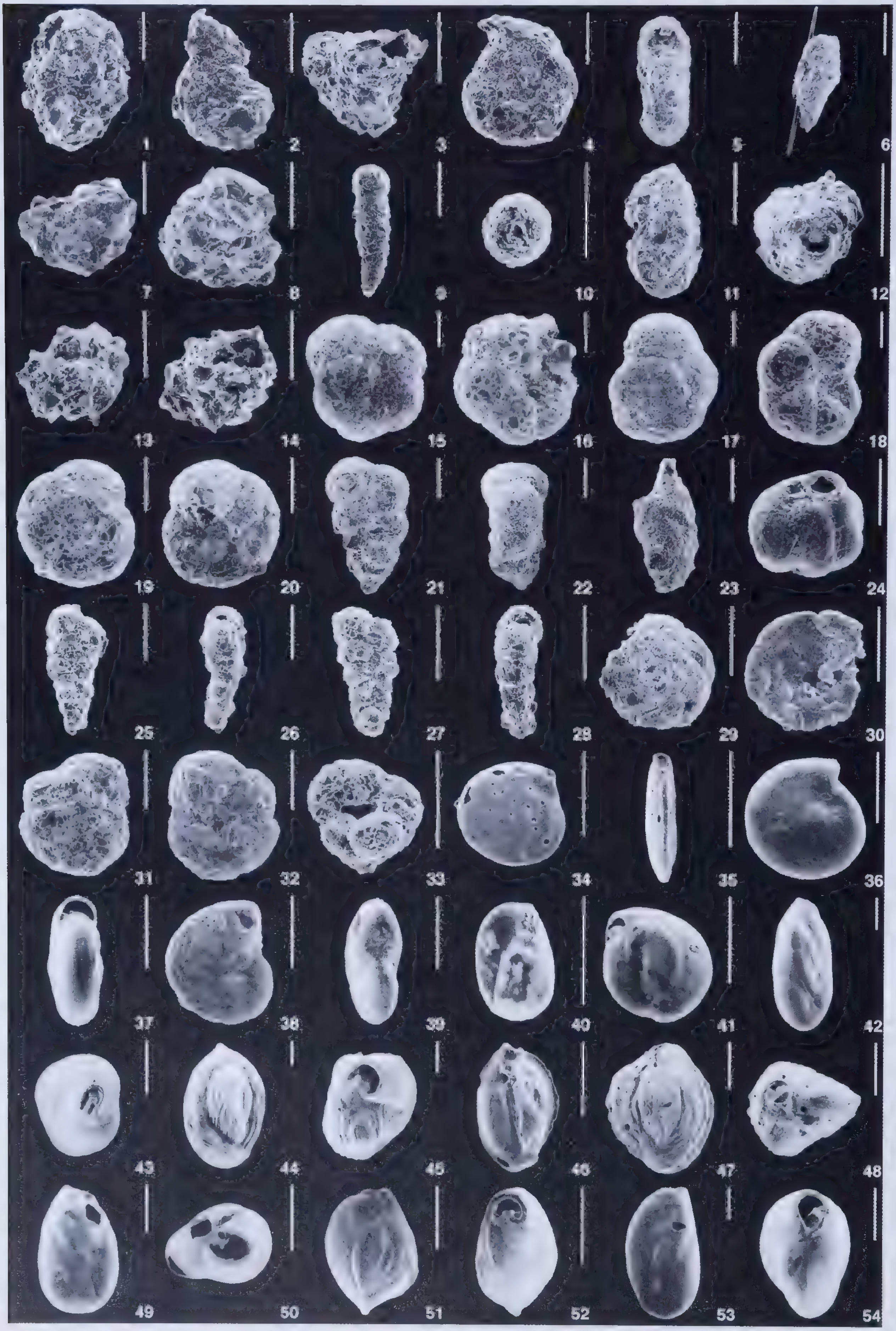
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Plate 2

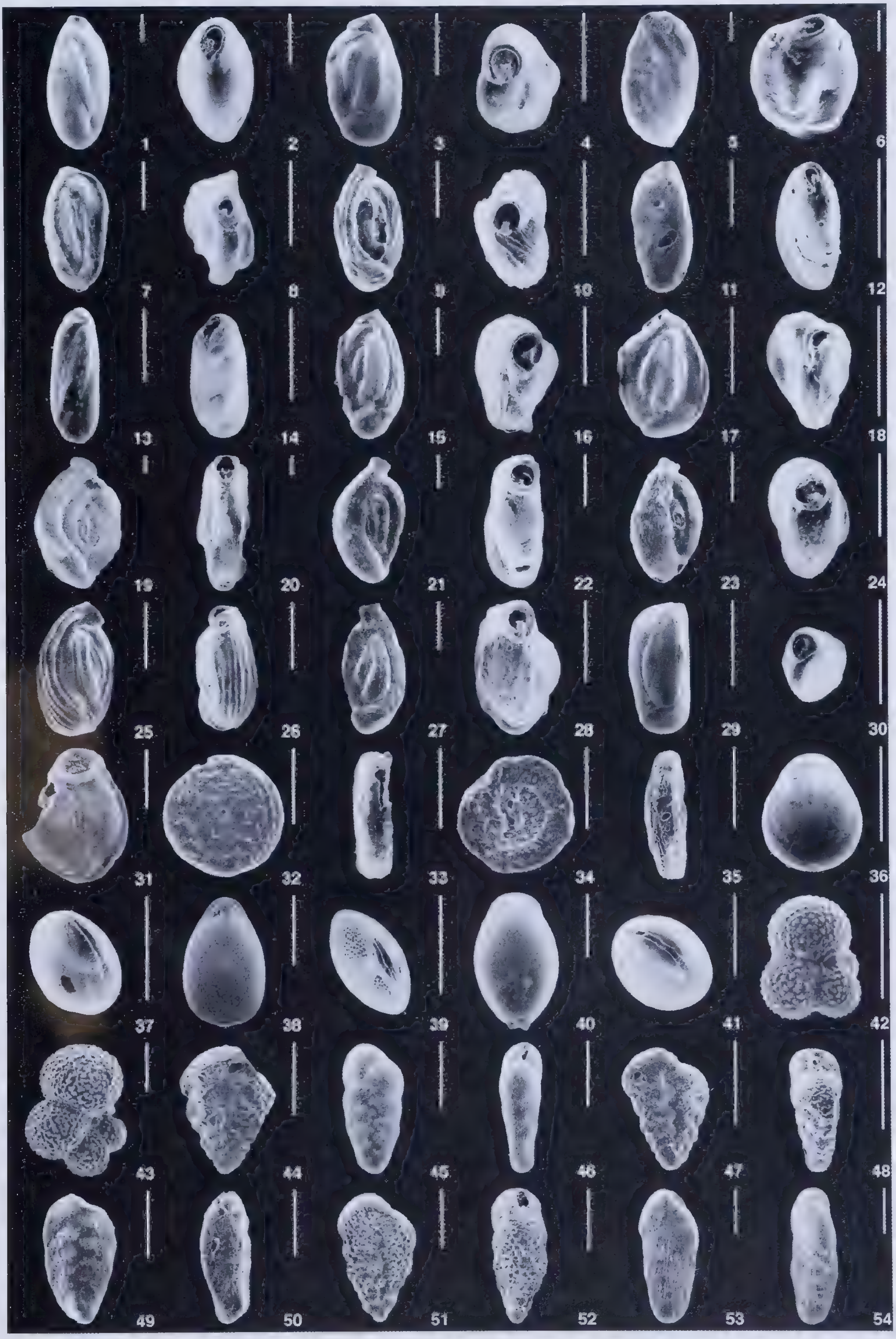
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Plate 3

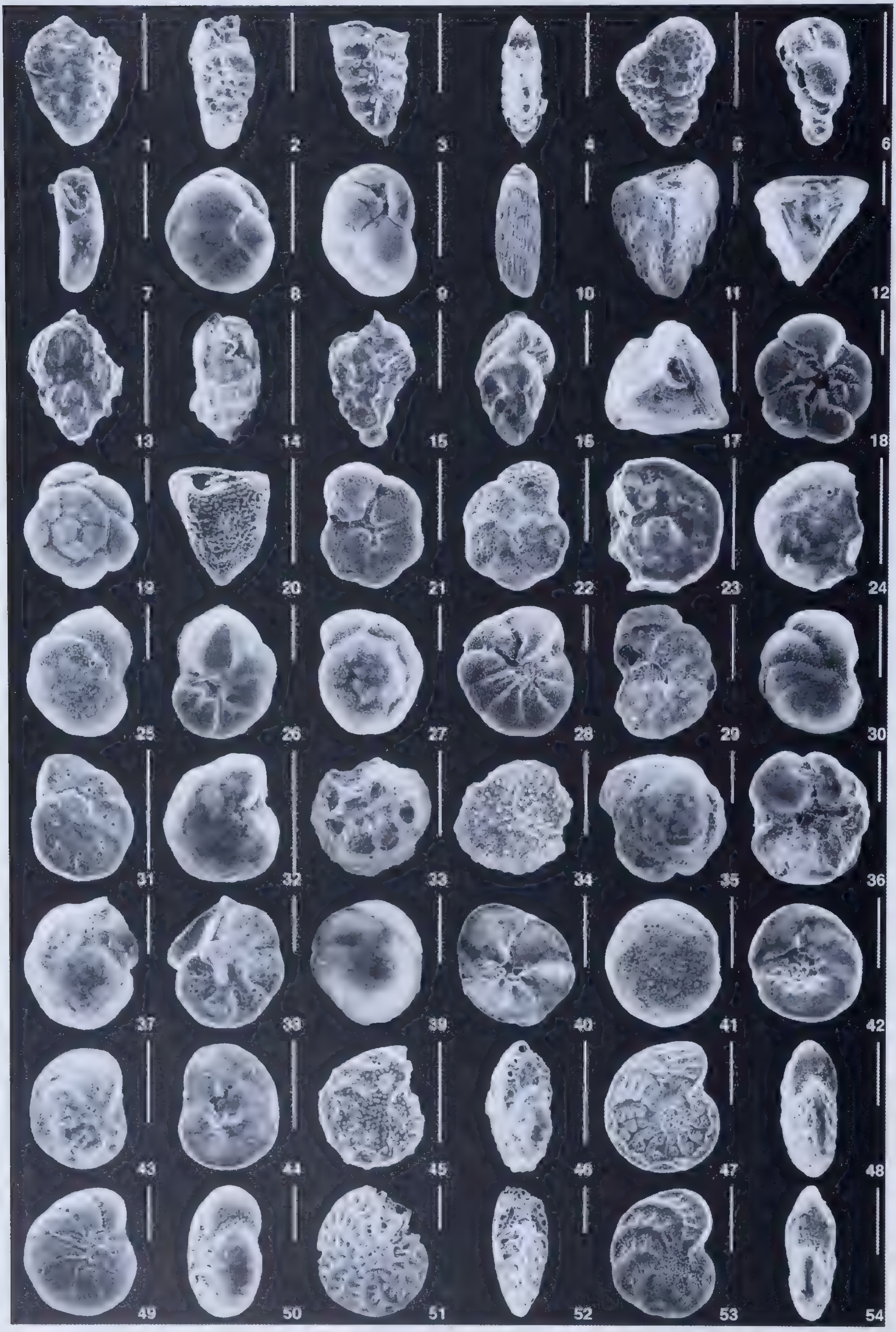
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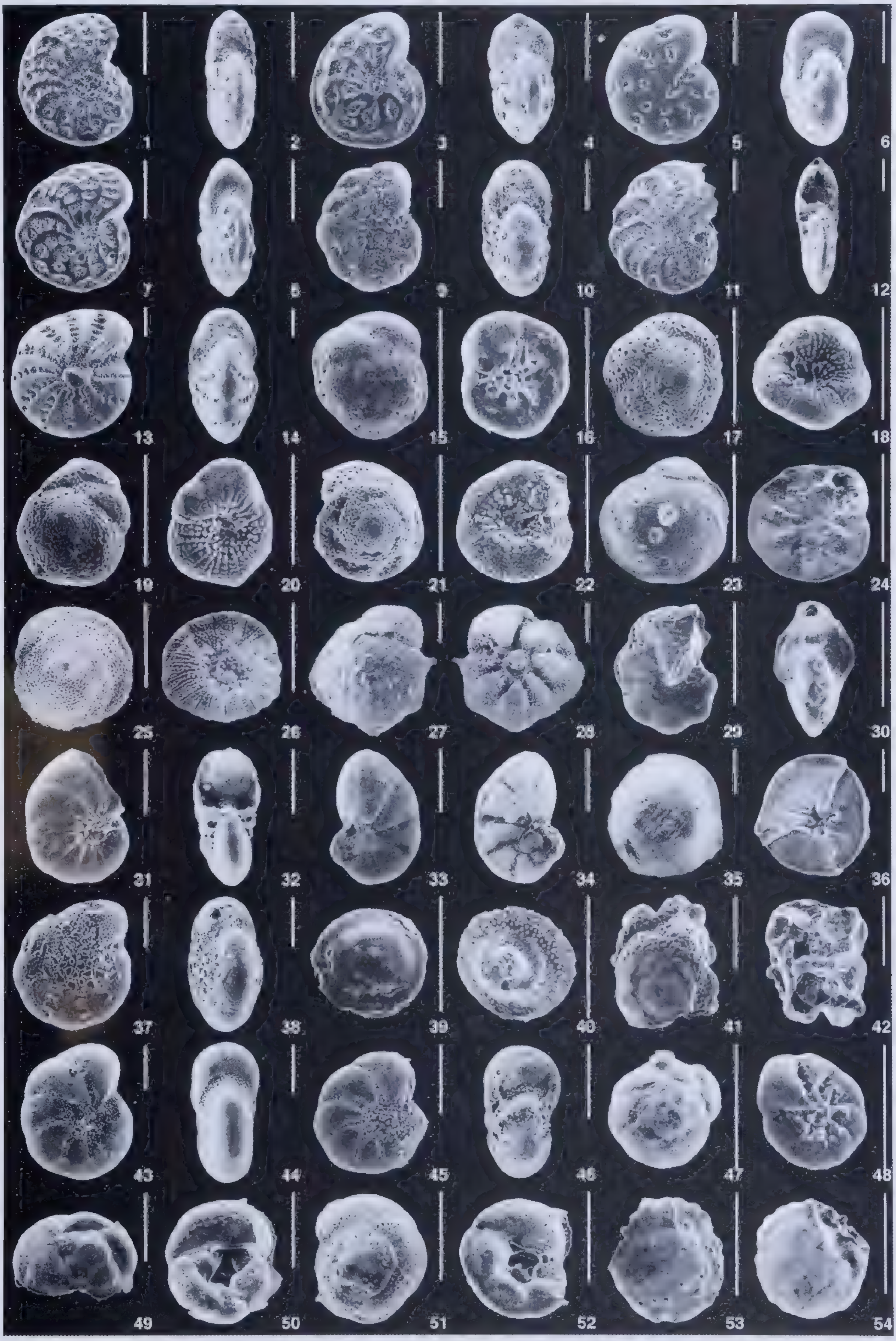
Plate 4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Molluscs of the Leschenault Inlet estuary: their diversity, distribution, and population dynamics

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Abstract

Thirty-one species of mollusc were collected in Leschenault Inlet during 1982-1987. Seven species were common, with the remaining 24 species occurring sporadically, rarely or only once during the study. These seven most common species in order of general abundance were: *Arthritica semen, Tellina deltoidalis, Nassarius burchardi, Spisula trigonella, Hydrococcus brazieri, Acteocina* sp and *Bedeva paivae*. The molluscs of Leschenault Inlet can be classified as follows: (1) a stenohaline marine component: *Bittium granarium, Mytilus edulis, Polinices conicus, Pholas australasiae, Nassarius nigellus, Solemya australis, Irus crenata*, and *Venerupis anomala*; (2) a euryhaline marine component: *Tellina deltoidalis, Tellina* sp, *Theora lubrica, Sanguinolaria biradiata, Philine angasi, Nassarius burchardi, Bedeva paivae, Spisula trigonella, Epicodakia* sp, and *Laternula creccina*; and (3) a true estuarine component: *Acteocina* sp, *Arthritica semen, Xenostrobus securis, Hydrococcus brazieri, Fluviolanatus subtorta, Assiminea* sp, and *Salinator* sp. Across the inlet in general, molluscs inhabited tidal sand or tidal mud, shallow water platform sand or muddy sand, or deep water basin mud, within lower, middle, or upper estuarine salinity fields. In this context, seven broadly recurring assemblages or populations of mollusc could be discerned: (1) a mixed molluscan assemblage inhabiting the tidally flushed environments of the Preston River Delta and the tidal delta leeward of "The Cut"; (2) a *Tellina* (± *Spisula*) assemblage inhabiting the deep water central muddy basin; (3) a *Tellina-Nassarius* (± *Bedeva*) assemblage inhabiting seagrass-vegetated platforms; (4) *Tellina* populations inhabiting shallow subtidal mud flats, (5) *Hydrococcus* populations inhabiting tidal sandy beaches; (6) *Acteocina* populations inhabiting tidal mud flats; and (7) *Arthritica* populations inhabiting low tidal to shallow subtidal sand flats. Population structures were found to be different for the three common genera. *Tellina* populations appeared to be maintained by a relatively continuous low level of juvenile recruitment. *Nassarius* populations were dominated by a mature age cohort, with a low intermittent level of juvenile recruitment. *Spisula* populations were numerically dominated by one age cohort, and were not maintained by further recruitment. This study provides a five-year perspective of changes in mollusc populations in Leschenault Inlet, providing insight into the variability and longevity of the fauna. Some species are consistently present in the estuary although abundances varied seasonally, while others fluctuated markedly in their presence or absence. While the overall character in terms of diversity/abundance, and population structure of the mollusc assemblages may have remained similar, there were also changes in composition from year to year and from season to season. For many species there was a decrease in abundance, such that the relative abundance of species within an assemblage changed with time. Abundances of each species fluctuated largely independently of other species or a given habitat, and did not apparently occur in response to seasonal patterns in oxygen concentration, temperature, or salinity.

Keywords: molluscs, Leschenault Inlet, estuary, population dynamics, south-western Australia.

Introduction

Estuarine molluscs have been studied to varying detail in south-western Australia (Ashman *et al.* 1969, Wilson 1969, Hughes 1973, Smith 1975, Wallace 1975, Chalmer *et al.* 1976, Poore & Rainer 1979, Brown *et al.* 1980, Wells *et al.* 1980, Rainer 1981, Wells & Threlfall 1981, 1982a,b,c; Chalmer & Scott 1984 Davey & George 1986). Specifically for Leschenault Inlet, molluscs were reported as part of a survey for benthic fauna in 1974 by Chalmer & Scott (1984), and by others who reported incidentally on them for comparative work (Smith 1975; Wells & Threlfall 1981). Most studies focused on the biology and occurrence of specific molluscs, and did not include details of habitats, molluscan assemblages in relation to habitat, or longer term population dynamics.

The dynamic physical and hydrochemical nature of the Leschenault Inlet estuary has developed a varied array of habitats across the system and a poikilosaline range of salinity fields, and this provides a context for describing and interpreting the distribution and abundances of estuarine molluscs. In contrast with most other studies into estuarine mollusc autoecology (cited above), the habitat framework of Wurm & Semeniuk (2000) is used here to view mollusc diversity, distribution, and population dynamics. Thus, this paper describes the mollusc assemblages of Leschenault Inlet over 5 years in terms of species composition and their relationship to habitat, the population dynamics of the more common species, and for three common species the dynamics of their population size structure.

Methods

Field study

The study of Leschenault Inlet and its molluscan fauna involved a range of sampling strategies, locations, and times

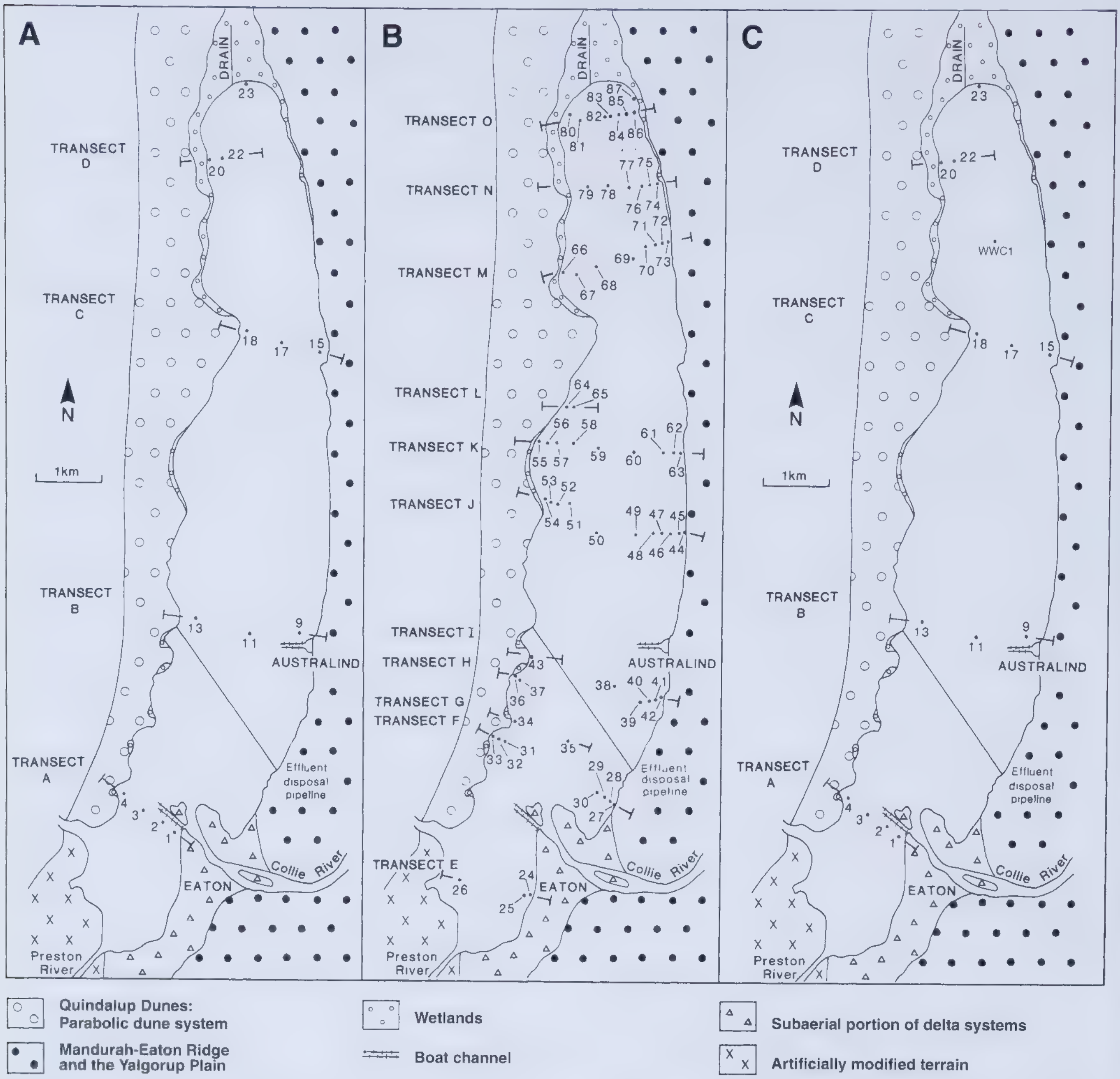

Figure 1. **A:** Location of the main fauna sampling transects and 22 sites. **B:** Location of the 63 supplementary fauna flora and substrate sampling sites. **C:** Location of the water sampling sites, and the estuarine salinity fields after Wurm & Semeniuk (2000).

over five years between 1982 and 1987. Physical and chemical habitat data were also collected and used to identify a number of habitats in the estuary (Wurm & Semeniuk 2000). A wide-ranging, reconnaissance survey was undertaken during February 1982 to identify the main habitat types, based on bathymetry, substrate, vegetation cover and hydrochemical setting. This survey was the basis for selection of 4 main east-west oriented sampling transects for molluscs (Fig 1A), representing various hydrochemical locations along the length of the estuary, and along which 22 main sampling sites were located and sampled between 1982 and 1987. The sampling sites were located at the most common habitat types. In December 1986, a supplementary survey of mollusc fauna was undertaken, involving an additional 63 sites located along a further 11 transects (Fig 1B).

During 1986 and 1987, estuarine water was sampled at sites along the 4 main transects. Salinity, oxygen concentration, and temperature were measured, as they were considered to be directly critical to benthos, and all samples and measurements were taken from the base of the water column. Initially, these water quality parameters were sampled at all 22 sites, but the number of sites was reduced later to between 2-4 per transect, comprising those sites considered representative of the general hydrochemical field for a given transect (Fig 1C). Water quality data, described in Wurm & Semeniuk 2000, also were used in this study.

Two methods were used for sampling molluscs. Except for the dedicated sampling of *Arthritica semen*, all species were sampled with a 25 cm x 25 cm x 25 cm box-corer.

Samples were washed in the field through a 1 mm mesh, and molluscs were counted, measured, and returned to the environment. Small species such as *Assiminea* sp and *Hydrococcus brazieri* were also counted by this method. *A. semen*, because of its small size and high abundance, was sampled with a cylindrical corer 10cm in diameter and 15cm long. Samples were washed through a 1 mm mesh, fixed in preservative, and counted in the laboratory to ensure that only live specimens were counted. From each site, replicate samples were collected within an homogeneous area of 5 m radius. Initially 10 replicate samples were collected, but for logistical reasons this was later reduced to five. At some sites where species density was very low, to obtain sufficient number of animals to construct population size frequency histograms, it was necessary to sample 20, and at times 40 replicates. For the survey in December 1986, only 3 replicate samples were taken as the data were used for mapping purposes and not population dynamics studies.

Population size structure was studied for *Nassarius burchardi, Tellina deltoidalis* and *Spisula trigonella.* These species were sufficiently abundant and large enough to readily allow investigation of juvenile recruitment and the relationship between population structure and abundance. Up to several hundred animals were typically measured during each survey. When abundance was low, sampling usually persisted until a minimum of 20 animals were collected. For *Nassarius*, the length of the shell from the spire tip to the posterior end of the columella was measured, and for bivalves the greatest length of the shell between posterior and anterior margins was measured. Measurement was carried out in the field, with the animals returned to their habitat after measurement. Although *Arthritica semens* was numerically the most abundant molluscan species in the estuary, its small size precluded the field approach outlined above for the other species. Study of *Arthritica semen* thus was a combined field and laboratory exercise. Samples of the species collected in small cores were returned to the laboratory, separated from seagrass, algae and other fauna such as polychaetes and small crustaceans under a binocular microscope, and then counted. The population size structure of this species was not analysed because the mesh size adopted for this study was 1 mm, and small individuals < 1mm in size (which were numerous and critical to the construction of size-frequency histograms) were not systematically sampled.

Monitoring of molluscs and habitat parameters was carried out annually, quarterly, or monthly (Table 1). Given the large number of sites involved, the anticipated medium

Table 1: Sampling times of fauna monitoring programmes.

DATE		SITE																					
		A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
I1982	FEB	.	.	.	.	.	.	.	.	S	.	.	S	S	S		.	.	.	.	.	.	.
	MAY	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	AUG	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1983	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	AUG	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	.
	DEC	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	.
1984	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	.	.	.
	AUG	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1985	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	.	.	.
	AUG	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1986	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	JUNE	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	JUL	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	AUG	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	SEP	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	OCT	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	NOV	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
1987	JAN	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	FEB	.	S	S	S	.	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	MAR	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S

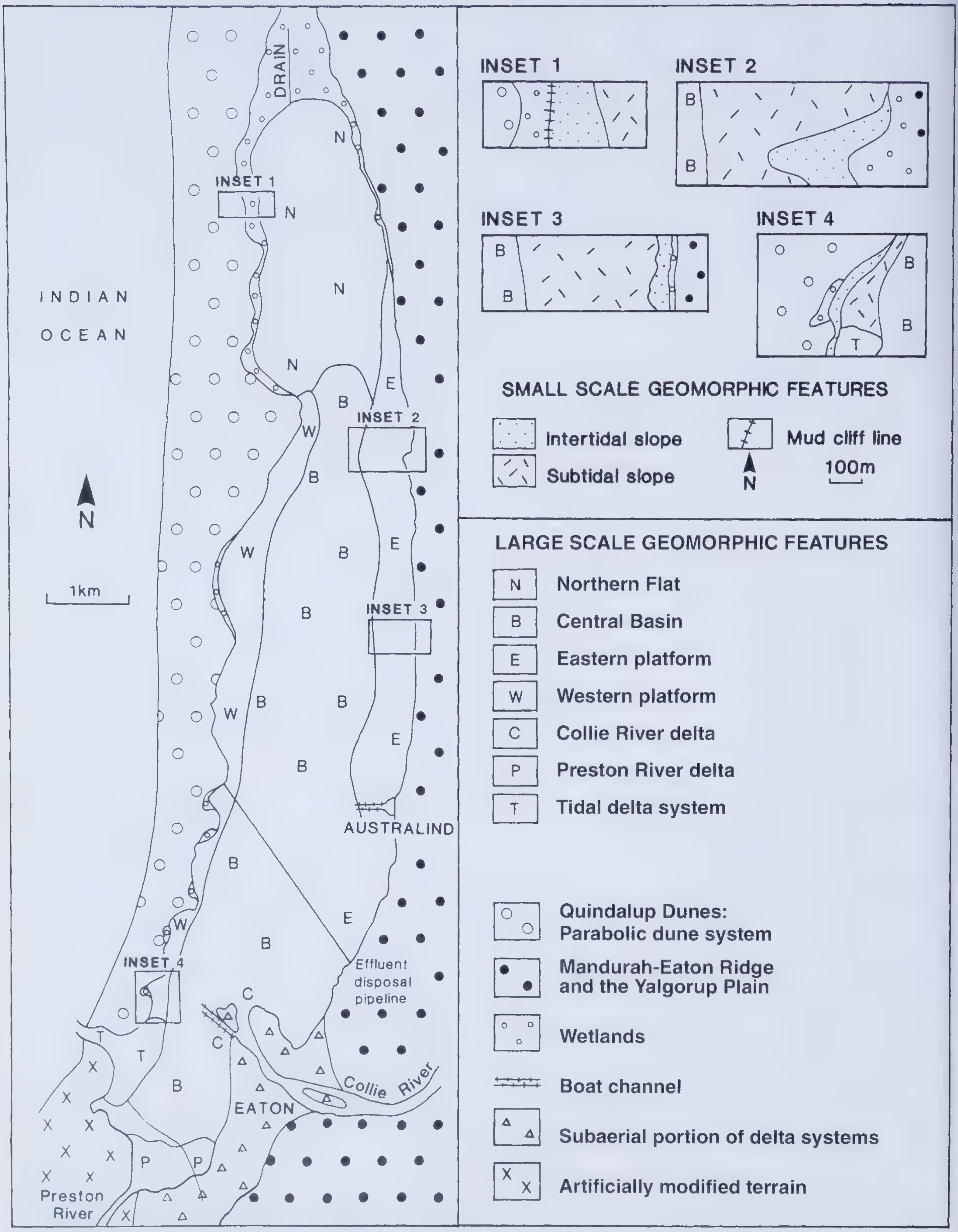

Figure 2. The large scale geomorphic/bathymetric units within Leschenault Inlet (after Wurm & Semeniuk 2000).

term faunal population monitoring proposed for this estuary dictated that a stratified sampling strategy be undertaken. After the initial reconnaissance survey in February 1982, for the period 1982-1986, all 22 sites were sampled in May 1982, representing an end-of-summer period, and thereafter sampled annually in February each year. Selected sites, representing examples of specific habitat settings in the four estuarine salinity fields, were sampled quarterly, representing seasonal sampling. After 1986, in the period February 1986 to March 1987, when the mollusc study became more intensive, the sites that were sampled yearly were then sampled quarterly, and the sites previously sampled quarterly were then sampled monthly. Monitoring sites thus can be categorised into two groups: those sampled frequently, *i.e.* quarterly between 1982 and 1986, and monthly between 1986 and 1987 (sites A2, A3, A4, B9, B11, B12, C15, C19, C17, D20, D21 and D22), and those sampled less frequently, *i.e.* yearly between 1982 and 1986, and quarterly between 1986 and 1987 (sites A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18). Data presented in this paper focus on that derived from the frequently sampled sites (A2, A3, A4, B9, B11, B12, C15, C19, C17, D20, D21 and D22) for seven key species. Data on these species for sites A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18 are presented in Appendix 1. The full data set for all sites and all species is presented in Wurm (1987). Sampling times are shown in Table 1.

Analytical methods

Abundances of animals, given as mean ± standard deviation, were determined from the box cores (surface area 625 cm^2) and the cylindrical corer (surface area *ca* 78 cm^2). These estimates were multiplied appropriately to calculate abundances per square meter. While the database of this study is large, encompassing regular sampling of 22 sites, most often seasonally for more than 5 years, many species were too sparse or too patchy for detailed study. Preliminary analyses of the main species were undertaken using a General Linear Model with replications, with the five sampling years and four sampling seasons selected as 'inner subject' factors, with substrate types, salinity field and depth as 'between subject' factors. Due to the large number of samples containing no specimens, data distributions were highly skewed, and even after square-root transformations were not normal-distributed according to Kolmogorov-Smirnov and Shapiro-Wilk tests. There was significant inhomogeneity of variances. Accordingly, the emphasis in this study is to focus on the mean density determined by the five replicates, and to compare these spatially and temporally.

Sample lodgement and database

Species were identified by S Slack-Smith and F Wells of the Western Australian Museum, and R Black of the Department of Zoology, University of Western Australia. Specimens of the taxa have been lodged with the Western Australian Museum. Raw data from this study, have been lodged with the Royal Society of Western Australia Library, in Microsoft Excel 5.0 spreadsheet and are available for future researchers.

Habitats of the Leschenault Inlet estuary

This study was confined to the subtidal and tidal area below the supratidal zone fringing the Leschenault Inlet Estuary. Within this area, the estuary can be divided into five bathymetric and geomorphic units (Fig 2; Table 2): (1) a relatively deep water central basin, underlain by mud; (2) a northern shallow water subtidal to tidal flat, underlain by mud; (3) a tidal to shallow water western platform/ramp underlain by muddy sand; (4) an eastern tidal to shallow water platform underlain mainly by sand; and (5) a delta, with subtidal prodelta sand flats, shoals, channels, and muddy bays. The estuary itself is a microtidal wave-dominated estuarine lagoon, with diurnal tides (mean range 0.5 m and a maximum range of 0.9 m; Semeniuk & Meagher 1981; Wurm & Semeniuk 2000). Waters within the estuary are poikilosaline (Fig 3). To the north, salinity varies annually from hyposaline to hypersaline. In the middle estuary, salinity fluctuates within a range of mesosaline values. At the Collie River delta, salinity varies from hyposaline to mesosaline. In winter, the salinity generally decreases with fresh water inflow from rivers, drains, run-off, and groundwater seepages (*e.g.* dunes and deltas). After winter, evaporation (induced by higher summer temperatures and wind) and the continued exchange with the ocean increase the water salinities. To the north, furthest away from "The Cut", estuarine waters may become hypersaline. Salinity is not typically stratified, but there is a salinity gradient from south to north over most seasons. Weak stratification exists, however, during times of freshwater influx.

The waters of the estuary generally are well oxygenated throughout the year (Fig 3). The highest oxygen values occur at the well-vegetated sites of shallow depths. Overall, there was no clear correlation between oxygen concentration and other water parameters, and oxygen concentration appeared to vary independently of temperature and salinity. Dissolved oxygen concentration even in summer is generally > 5 mg L^{-1}. Water temperatures of the estuary in winter in deep water are frequently below 15 °C; summer temperatures are frequently at or above 25 °C, but generally around 22 °C. The deep water of the central basin has a temperature range of *ca* 10 °C, and is generally maintained at a lower temperature than shallower sites. Shallower water sites have winter water temperatures of *ca* 15 °C, and summer temperatures of *ca* 30 °C. They also exhibit greater temperature fluctuations. Shallow water sites, with dark muddy substrates had the highest temperatures, up to 32 °C.

The water body of the estuary can be divided into 4 gradational salinity fields based on mean salinity value and its variation throughout the year (Fig 4; Wurm & Semeniuk 2000). This also formed the basis for dividing the estuary into large scale habitat settings: (1) a deltaic field where mean salinity is slightly less than that of sea water but with a large variability about the mean (Transect A); (2) lower estuarine field in which mean salinity is slightly greater than that of sea water, with a small variability about the mean (Transect B); (3) a mid estuarine field in which mean salinity is higher than that of sea water, with a large variability about the mean (Transect C); and (4) an upper estuarine field in which mean salinity is much greater than

Table 2. Main features of the habitat types of Lescenault Inlet.

Habitat Type	Distribution across large scale geomorphic unit	Salinity field*	Vegetation cover	Depth	Substrate	Site samples and other features
deltaic inter-tidal sand	Collie River delta	hyposaline to mesosaline	none	0-0.25m	medium to course sand	A1, A6, A7
deltaic sand	Collie River delta	hyposaline to mesosaline	none	0.25-0.50m	Medium to course sand	A2
lower-estuarine basinal mud	central basin	mesosaline stable	none or patchy *Halophila ovalis*	1-2m	mud	B11, B12, G35
lower-estuarine basinal	central basin	mesosaline stable	none or patchy *Halophila ovalis*	1-1.5m	sandy mud	A3, H38, the sand fractions are comprised predominately of fossil gastropod shells
lower-estuarine platform sand	eastern platform as a shore-parallel ribbon to 500m; western platform as an apron emanating from front of parabolic dunes	mesosaline stable	continuous *Halophila ovalis* some *Ruppia megacarpa*, and *Gracilaria* sp, rare *Heterozostera tasmanica*	0.25 - 1m	medium sand to muddy medium sand	B8, E25, E26, F28, F29, F30, the western platform the unit is developed at the reworked front of encroaching dunes
lower-estuarine platform mud	western platform as an irregular shore-parallel ribbon	mesosaline, stable	continuous *Halophila ovalis* cover with *Gracilaria* sp	0.25-1m	mud to sandy- mud and shelly-mud	B14, F31, F32, H36, H37
lower-estuarine intertidal mud	westerm platform as an irregular shore-parallel ribbon to 50m wide	mesosaline stable	none	0-0.25m	mud; may overly sandy-mud	F33 developed in sheltered embayments pools of water are retained at low tide because of the undulating surface shallow
lower-estuarine intertidal sand	eastern platform, shore- parallel ribbon 50-100m; western platform shore-parallel ribbon or apron 10-30m wide	mesosaline stable	none	0-0.25m	medium sand	E24, F27, H42; on the western platform the unit is developed at the reworked front of encroaching dunes
lower-estuarine platform muddy-sand	western platform as an irregular shore- parallel ribbon	mesosaline stable	continuous *Halophila ovalis* cover with *Gracilaria* sp	0.25-1m	muddy medium sand	A4, A5, B9, B10, B13
mid-estuarine basinal mud	central basin	mesosaline fluctuating	none or patchy *Halophila ovalis*	1-1.6m	mud to sandy-mud	C17, J49, J50, K59, K60
mid-estuarine platform mud	western platform, shore-parallel ribbon to 500m	mesosaline, fluctuating	continuous *Halophila ovalis* cover with algae	0.25-1m	mud to sandy-mud	C18, J51, K56, K57, K58, L65

Table 2 (continued). Main features of the habitat types of Lescenault Inlet.

Habitat Type	Distribution across large scale geomorphic unit	Salinity field*	Vegetation cover	Depth	Substrate	Site samples and other features
mid-estuarine platform muddy-sand	western platform, share-parallel ribbon to 300m wide; eastern platform, shore-parallel ribbon 300m wide	mesosaline, fluctuating	continuous *Halophila ovalis* cover with *Chaetomorpha* sp and *Gracilaria* sp	0.25-0.70m	muddy medium sand	C15, C16, J52, J53, J54
mid-estuarine platform sand	eastern platform, shore-parallel ribbon to 500m	mesosaline fluctuating	continuous *Halophila ovalis* with some algae	0.25-0.90cm	medium sand	J45, J46, J47, J48, K61, K62
mid-estuarine intertidal muddy-sand	western platform, apron or shore-parallel ribbon to 30m	mesosaline fluctuating	none	0-0.25m	muddy medium sand	K55, L64
mid-estuarine intertidal sand	eastern platform, shore-parallel ribbon to 100m wide	mesosaline fluctuating	none	0-0.25m	medium sand	C19, J44, K63
upper-estuarine flat sand	northern flat shore-parallel rion 100-200m wide	hyposaline to hypersaline	sparse *Acetabularia* sp	0.05-0.30m	medium sand to muddy medium sand	N72, N75
upper-estuarine flat mud	northern flat, the shallow centre wide	hyposaline to hypersaline	patchy to continuous cover of *Halophila ovalis*	0.30-0.55m	mud to sandy- mud	M68, M69, M70, M71, N76 N77, N78, N79
upper-estuarine intertidal sand	northern flat, shore-parallel ribbon to 150m wide	hyposaline to hypersaline	none	0-0.25m	medium sand to muddy medium sand	M72, M73, N74, N75, O86
upper-estuarine intertidal mud	northern flat as a shore-parallel ribbon up to 400m wide	hyposaline to hypersaline	none or sparse and patchy *Chaetomorpha* sp *Gracilaria* sp; or some *Ruppia megacarpa*	0-0.30m	mud and sandy mud	D20, D21, D22, M66, M67, O80, O81, O82, O83, O84, O85; because of the undulating surface shallow pools of water are retained at low tide.

*Terminology after Hammer (1986).

that of sea water, with a very large variability about the mean (Transect D).

In the descriptions of sampling sites that follow in relation to the molluscs, site numbers prefixed by A along Transect A are in the deltaic salinity field, those prefixed by B are along Transect B in the lower estuarine salinity field, those prefixed by C are along Transect C in the middle estuarine salinity field, and those prefixed by D are along Transect D in the upper estuarine salinity field.

Wurm & Semeniuk (2000) also divide the estuary into some 19 habitat units for benthic biota (Fig 4), based on geomorphology, substrates, depth, and hydrochemistry. A summary description of habitat features of the 22 sampling sites is provided in Table 3.

The molluscs of Leschenault Inlet estuary

Diversity & Distribution

Thirty-one species of mollusc were collected in Leschenault Inlet during the study period (Table 4). Of these, only 14 were recorded by Wells & Threlfall (1981) in their survey of the Peel-Harvey Estuary, with 20 recorded

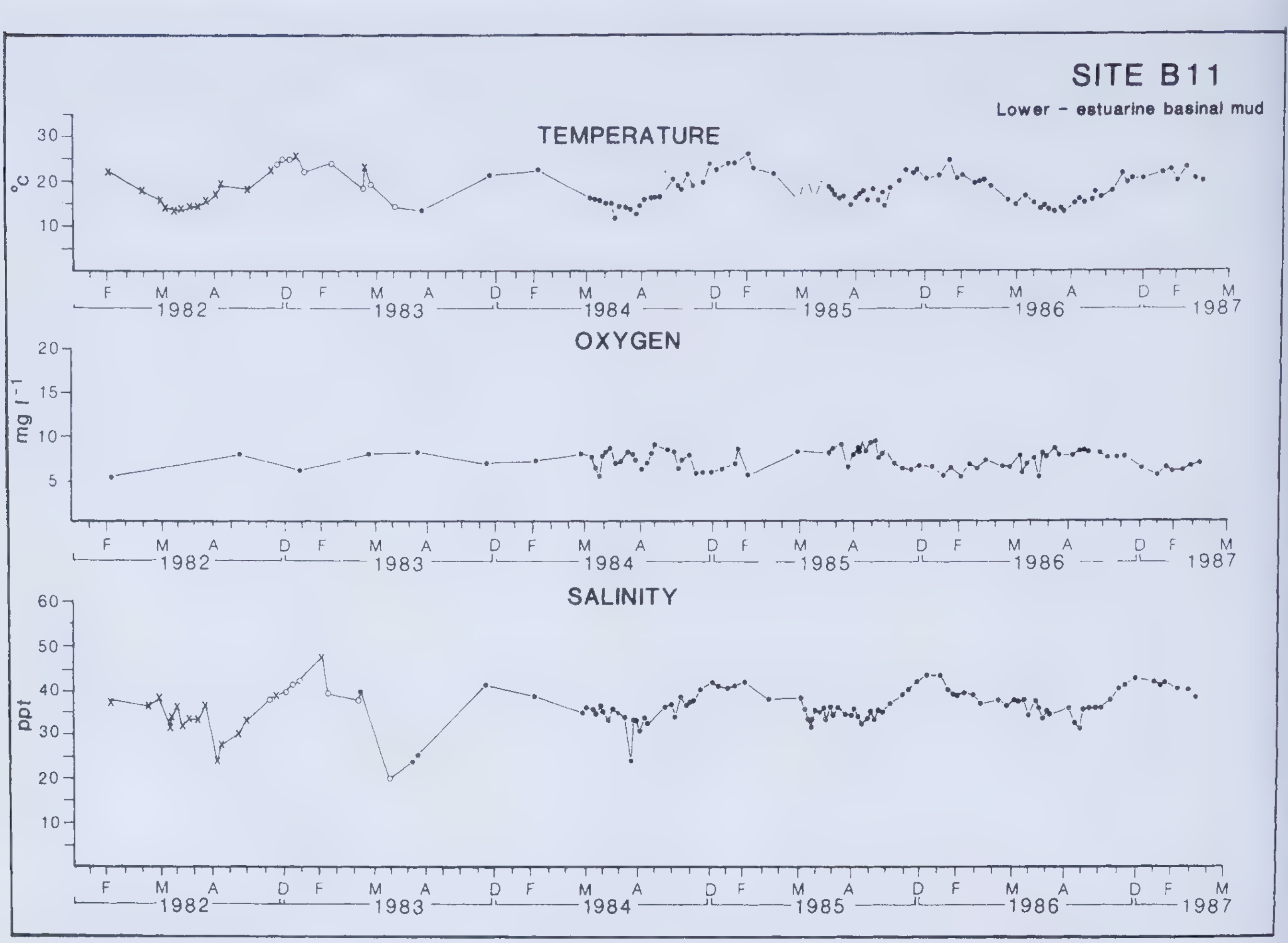

Figure 3. Typical variation of water temperature, oxygen, and salinity in the middle estuary, showing seasonal; fluctuation of temperature and salinity. Data from site B11 (see Fig 1A; after Wurm & Semeniuk 2000).

by Chalmer *et al.* (1976) for the Swan River Estuary. In Leschenault Inlet, during this study, seven mollusc species were common, with the remaining 24 species occurring sporadically, rarely or only once during the study. In order of decreasing abundance, these seven most common species are: *Arthritica semen*, *Tellina deltoidalis*, *Nassarius burchardi*, *Spisula trigonella*, *Hydrococcus brazieri*, *Acteocina* sp, and *Bedeva paivae*. Although not common throughout the estuary, *Assiminea* sp and *Xenostrobus securis* were sufficiently abundant at all times or abundant sporadically to warrant a brief description in this paper. Most of the uncommon, rare, restricted, or sporadically occurring species fall into 5 groups:

1. Species occurring only in the marine-influenced southern sites of the estuary near the opening to the ocean (Transect A) frequently occurred only as juveniles. It is probable they have developed from oceanic larvae originating from outside the Inlet. This group included the largest number of species, *viz. Donax columbella*, *Epicodakia* sp, *Irus crenata*, *Mactra flindersi*, *Mytilus edulis*, *Nassarius nigellus*, *Pholas australasiae*, *Polinices conicus*, *cf Solemya australis*, and *Venerupis galactites*.

2. Species occurring infrequently or rarely, but not confined to sites near the opening of the estuary to the ocean, included *Fluviolanatus subtorta*, *Laternula creccina*, *Philine angasi*, *Salinator* sp, *Tellina* sp, *Theora lubrica*, and *Venerupis anomala*.

3. Species which were present throughout the study period and across much of the estuary, but in low numbers, included *Assiminea* sp, *Bedeva paivae*, and *Sanguinolaria biradiata*.

4. Species forming small local populations at a single site for a short period include *Xenostrobus securis*, which occurred on deltaic sands of the Collie River delta at the beginning of the study, and *Bittium granarium* which was established late in the study along Transect C on the western platform.

5. One species (*Bembicium auratum*) forming small local populations over a long period at a single site (within local a mangrove environment along the intertidal shore of the estuary).

Abundance and age structure

Data on the abundance, temporal variation of the most common mollusc species, and the age structure of three species are shown in Figs 5-14, and described below in regard to environmental factors and population age structure for selected species. The description of mollusc abundances centres around the results of the most frequently monitored sites *i.e.* A2, A3, A4, B9, B11, C15,

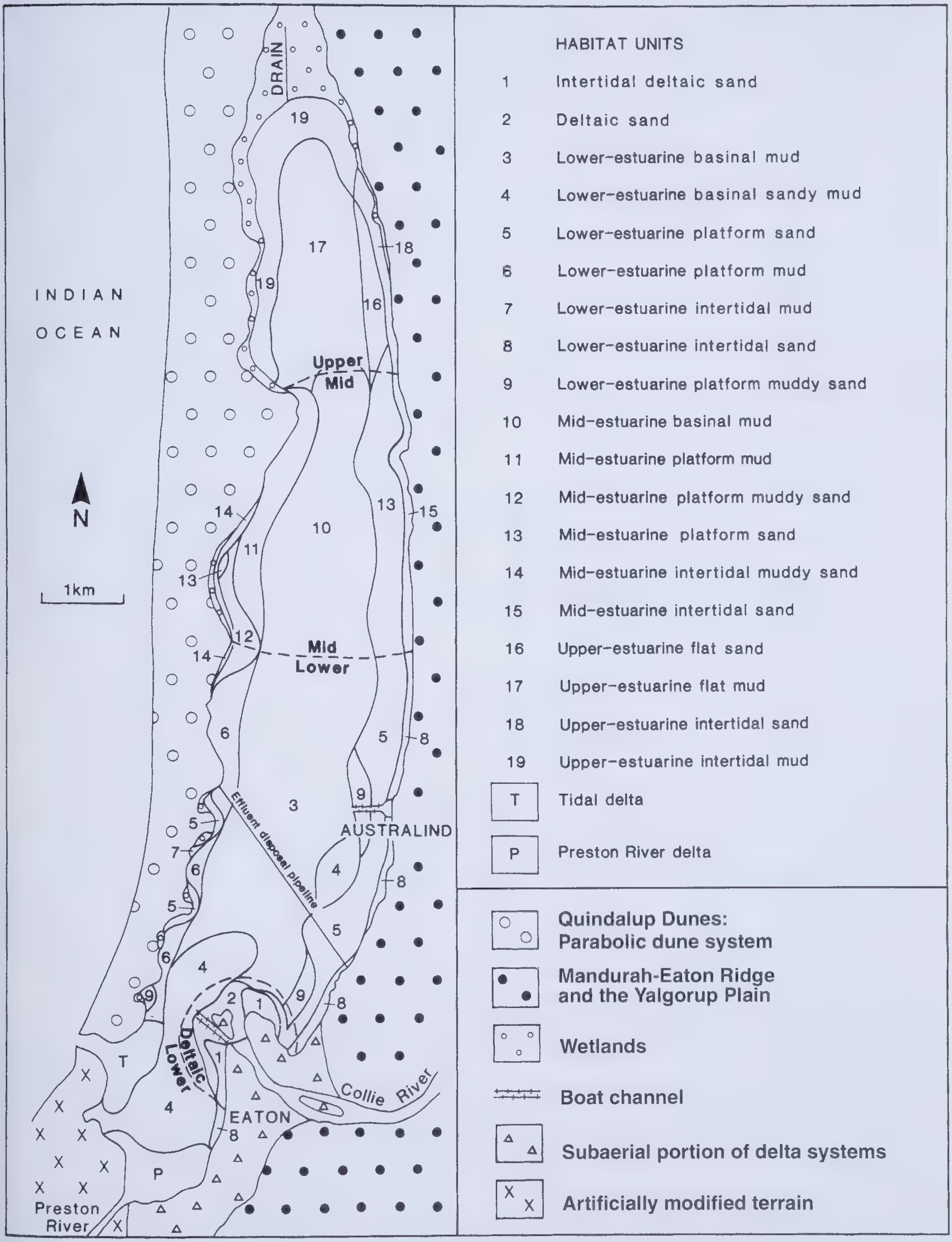
INDIAN
OCEAN
N
1km
DRAIN
19
17
18
19
16
Upper
Mid
13
15
14
10
11
13
12
Mid
Lower
14
6
5
8
9
3
Effluent disposal pipeline
AUSTRALIND
5
7
6
4
8
5
5
6
4
9
2
1
9
8
T
Deltaic
Lower
1
X
4
Collie River
EATON
8
P
Preston
River
HABITAT UNITS
1 Intertidal deltaic sand
2 Deltaic sand
3 Lower-estuarine basinal mud
4 Lower-estuarine basinal sandy mud
5 Lower-estuarine platform sand
6 Lower-estuarine platform mud
7 Lower-estuarine intertidal mud
8 Lower-estuarine intertidal sand
9 Lower-estuarine platform muddy sand
10 Mid-estuarine basinal mud
11 Mid-estuarine platform mud
12 Mid-estuarine platform muddy sand
13 Mid-estuarine platform sand
14 Mid-estuarine intertidal muddy sand
15 Mid-estuarine intertidal sand
16 Upper-estuarine flat sand
17 Upper-estuarine flat mud
18 Upper-estuarine intertidal sand
19 Upper-estuarine intertidal mud
T Tidal delta
P Preston River delta
Quindalup Dunes: Parabolic dune system
Mandurah-Eaton Ridge and the Yalgorup Plain
Wetlands
Boat channel
Subaerial portion of delta systems
Artificially modified terrain

Figure 4. Distribution of habitats in the Leschenault Inlet estuary.

Table 3. Habitat features of sites on Transects A-D.

Site	Large-scale geomorphic unit	Habitat unit	Substrate	Flora	Salinity
A1	Collie River Delta	Deltaic inter-tidal sand	Medium & coarse sand	None	Deltaic
A2	Collie River Delta	Deltaic sand	Medium & coarse sand	None	Deltaic
A3	Central Basin	Lower estuarine basinal sandy mud	Sandy mud	Patchy *Halophila*	Lower
A4	Western Platform	Lower estuarine platform muddy sand	Muddy medium sand	*Halophila*	Lower
A5	Western Platform	Lower estuarine inter-tidal muddy sand	Muddy medium sand	Patchy algae & *Halophila*	Lower
A6	Collie River Delta	Deltaic inter-tidal sand	Medium & fine sand	Patchy algae & *Halophila*	Lower
A7	Collie River Delta	Deltaic inter-tidal sand	Medium & fine sand	Patchy algae & *Halophila*	Lower
B8	Eastern Platform	Lower estuarine platform sand	Medium sand	Patchy *Halophila* & algae	Lower
B9	Eastern Platform	Lower estuarine platform muddy sand	Medium sand	*Halophila*	Lower
B10	Eastern Platform	Lower estuarine platform muddy sand	Medium sand	*Halophila*	Lower
B11	Central Basin	Lower estuarine basinal mud	Mud	Patchy *Halophila*	Lower
B12	Central Basin	Lower estuarine basinal mud	Mud	Patchy *Halophila*	Lower
B13	Western Platform	Lower estuarine platform muddy sand	Muddy medium sand	*Halophila* & algae	Lower
B14	Western Platform	Lower estuarine platform sandy mud	Sandy mud	Patchy algae & *Halophila*	Lower
C15	Eastern Platform	Mid estuarine muddy sand	Muddy medium sand	*Halophila* & algae	Mid
C16	Eastern Platform	Mid estuarine muddy sand	Muddy medium sand	*Halophila* & algae	Mid
C17	Central Basin	Mid estuarine basinal mud	Mud	Patchy *Halophila*	Mid
C18	Western Platform	Mid estuarine platform sandy mud	Mud	*Halophila* & algae	Mid
C19	Eastern Platform	Mid estuarine inter-tidal sand	Medium sand	None	Mid
D20	Northern Flat	Upper estuarine inter-tidal sandy mud	Sandy mud	Patchy algae	Upper
D21	Northern Flat	Upper estuarine inter-tidal mud	Mud	Patchy algae	Upper
D22	Northern Flat	Upper estuarine inter-tidal mud	Mud	Patchy algae	Upper

C17, C19, D20 and D22. Data for the other sites are presented in Wurm (1987). The distribution and relative abundance of the main species with respect to the identified habitats are described in Table 4.

Figure 15 shows the distribution and relative abundance of key species during estuary-wide sampling in December 1986. This information presents a single time frame and was obtained when a number of species were increasing in their abundance within the estuary after a period of relatively low population densities over the period 1984 to mid 1986. The distribution of species with respect to habitat and setting in the estuary is summarised in Figure 16, as based on the results of the longer term sampling. In December 1986, *Acteocina* was located mainly in the tidal to subtidal upper estuary, and to a less extent along the tidal shore of the eastern platform. *Arthritica semen* was located on the tidal and subtidal shallow water platform environments in all salinity fields, with local abundances reaching thousands per square metre. *Assiminea* was restricted to the tidal to shallow water upper estuary. *Hydrococcus brazieri* was located mainly in the tidal to subtidal upper estuary and patchily along the tidal and shallow water environments of the eastern platform. *Nassarius burchardi* was widespread throughout the estuary, but generally absent from the northern basin. *Tellina*

Table 4. Species listing and their main occurrence in habitats of the estuary.

Species	Main habitats	Relative abundance within habitat 1982-1987
AMPHIBOLIDAE		
Salinator sp	upper-estuarine intertidal mud; one recording at site D20.	uncommon
ASSIMINEIDAE		
Assiminea sp	upper-estuarine intertidal mud; mid-estuarine muddy-sand.	uncommon
CERTHIDAE		
Bittium granarium (Kiener, 1842)	lower-estuarine platform muddy-sand; at site A4.	uncommon, becoming common at that site during the monitoring
CERITHIOPSIDAE		
unidentified species	lower-estuarine platform muddy-sand; one specimen recorded at A4.	uncommon
DONACIDAE		
Donax columbella Lamarck, 1818	tidal delta; one recording.	uncommon
HYDROCOCCIDAE		
Hydrococcus brazieri (Tenison Woods, 1876)	upper-estuarine flat mud; mid-estuarine intertidal sand; mid-estuarine platform muddy-sand.	common
LATERNULIDAE		
Laternula creccina Reeve, 1860	mid-estuarine intertidal sand; one recording at site C19; lower-estuarine platform muddy-sand; one recording at site A4.	uncommon
LEPTONIDAE		
Arthritica semen (Menke, 1843)	upper-estuarine intertidal mud; mid-estuarine platform muddy-sand; mid-estuarine intertidal muddy-sand; lower-estuarine platform sand; lower-estuarine intertidal sand; lower-estuarine intertidal mud; deltaic sand; deltaic intertidal sand.	common
LITTORINIDIDAE		
Bembicium auratum (Quoy & Gaimard, 1834	at the contact between marshlands and lower-estuarine intertidal deltaic sand, and in mangrove zone.	uncommon
LUCINIDAE		
Epicodakia sp	lower-estuarine basinal sandy-mud; one recording at site A3.	uncommon
MACTRIDAE		
Mactra flindersi Cotton, 1938	lower-estuarine platform muddy-sand; one recording at site A4.	uncommon
Spisula trigonella (Lamarck, 1818)	mid-estuarine basinal mud; mid-estuarine intertidal sand; lower-estuarine basinal initially common, mud, lower-estuarine basinal sandy-mud; deltaic sand.	common only at beginning of monitoring; later uncommon
MURICIDAE		
Bedeva paivae (Crosse, 1864)	upper-estuarine peripheral mud; mid-estuarine basinal mud; lower-estuarine platform sand; deltaic sand.	common-uncommon
MYTILIDAE		
Mytilus edulis (Lamarck, 1819)	deltaic sand, one recording at site A2.	uncommon

Table 4 (continued). Species listing and their main occurrence in habitats of the estuary.

Species	**Main habitats**	**Relative abundance within habitat 1982-1987**
Xenostrobus securis (Lamarck, 1819)	deltaic sand and deltaic intertidal sand.	common for a short period; no longer present at end of monitoring period
NATICIDAE		
Polinices conicus (Lamarck, 1822)	lower-estuarine basinal sandy-mud; several recordings of one or two individuals at site A3.	uncommon
NASSARIIDAE		
Nassarius burchardi (Philippi, 1849)	occurs in all subtidal habitats in the mid-estuarine and lower-estuarine salinity fields.	common
Nassarius nigellus (Reeve, 1854)	lower-estuarine platform sand; one recording in lower-estuarine basinal mud at site A3.	uncommon
PHILINIDAE		
Philine angusi (Crosse & Fischer, 1865)	lower-estuarine basinal sandy-mud one recording at site A3; mid-estuarine intertidal sand, one recording at site C19.	uncommon
PHOLADIDAE		
Pholas australasiae Sowerby, 1849	basinal sandy-mud, one recording at site A3; deltaic sand, on recording at site A2.	uncommon
SANGUINOLARIIDAE *Sanguinolaria biradiata* (Wood 1815)	mid-estuarine platform muddy-sand, lower-estuarine platform sand.	common-uncommon
SCAPHANDRIDAE *Acteocina* sp	upper-estuarine intertidal mud, mid-estuarine intertidal sand.	common
SEMELIDAE *Theora lubrica* Gould, 1861	mid-estuarine and lower-estuarine basinal muds, and lower-estuarine basinal sandy-mud.	uncommon
SOLEMYIDAE cf *Solemya australis* Lamarck, 1818	lower-estuarine platform mud and lower-estuarine basinal sandy-mud.	uncommon
TELLINIDAE		
Tellina deltoidalis (Lamarck, 1818)	common in all subtidal habitats, less common in upper-estuarine intertidal and flat mud.	common
Tellina sp	one recording in upper-estuarine intertidal mud.	uncommon
TRAPEZIIDAE Fluviolanatus subtorta (Laseron, 1956)	upper-estuarine intertidal mud; one recording at site D20.	uncommon
VENERIDAE		
Irus crenata (Lamarck, 1818)	deltaic sand, several recordings at site A2; single on lower-estuarine basinal mud, platform sand and platform mud.	uncommon
Katelysia sp	one recording on lower-estuarine basinal sandy-mud.	uncommon
Venerupis anomala (Lamarck, 1818)	deltaic sand, two recordings at site A2; also single recordings on lower-estuarine basinal sandy-mud, sand and lower-estuarine platform mud.	uncommon
Venerupis galactites (Lamarck, 1818)	lower-estuarine basinal sandy-mud, one recording at site A3.	uncommon

LEPTONIDAE: *Arthritica semen*

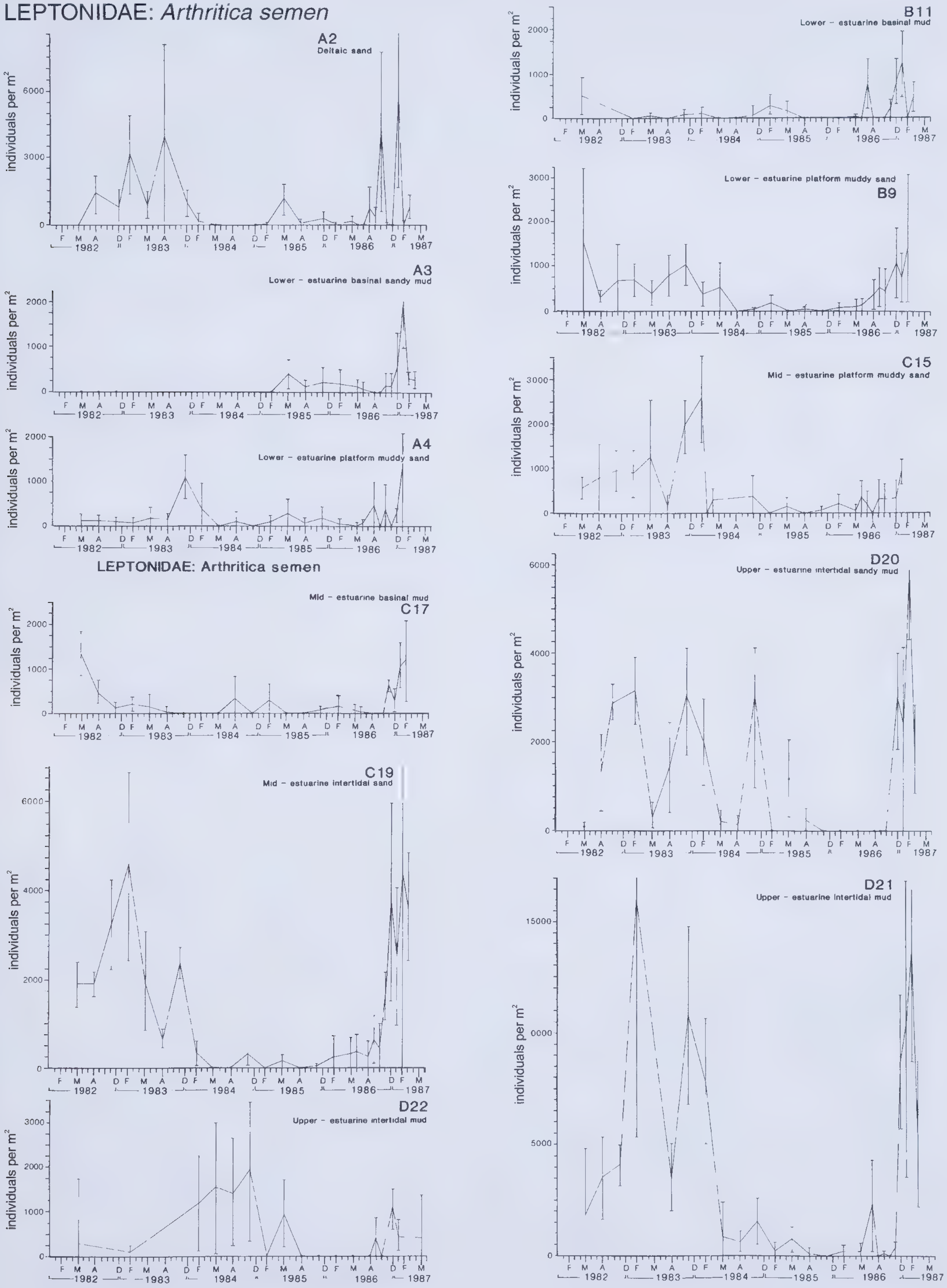

Figure 5. Abundance of individual per m^2 (mean ± sd) for *Arthritica semen* at the key sampling sites.

TELLINIDAE: *Tellina deltoidalis*

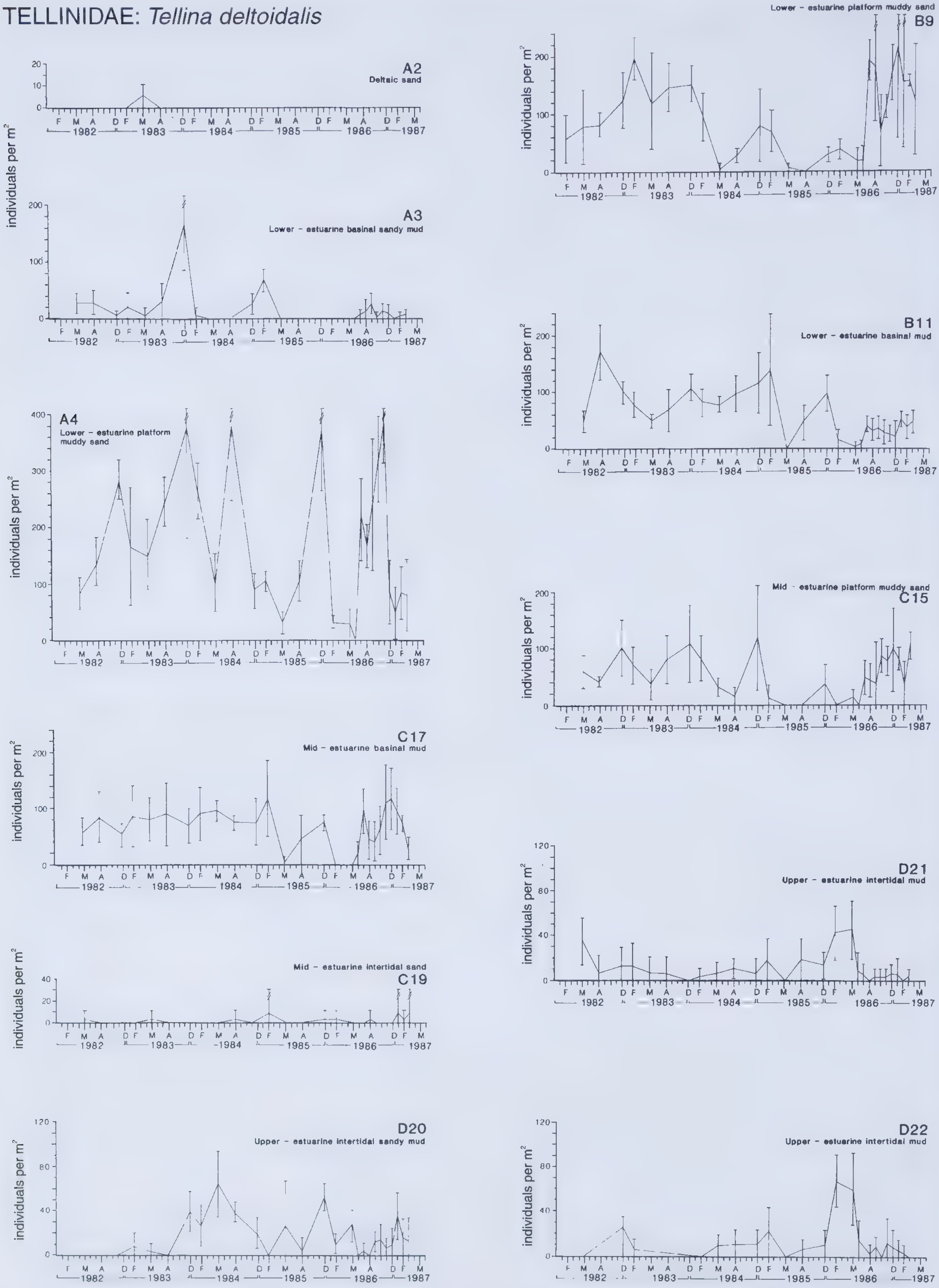

Figure 6. Abundance of individual per m^2 (mean ± sd) for *Tellina deltoidalis* at the key sampling sites.

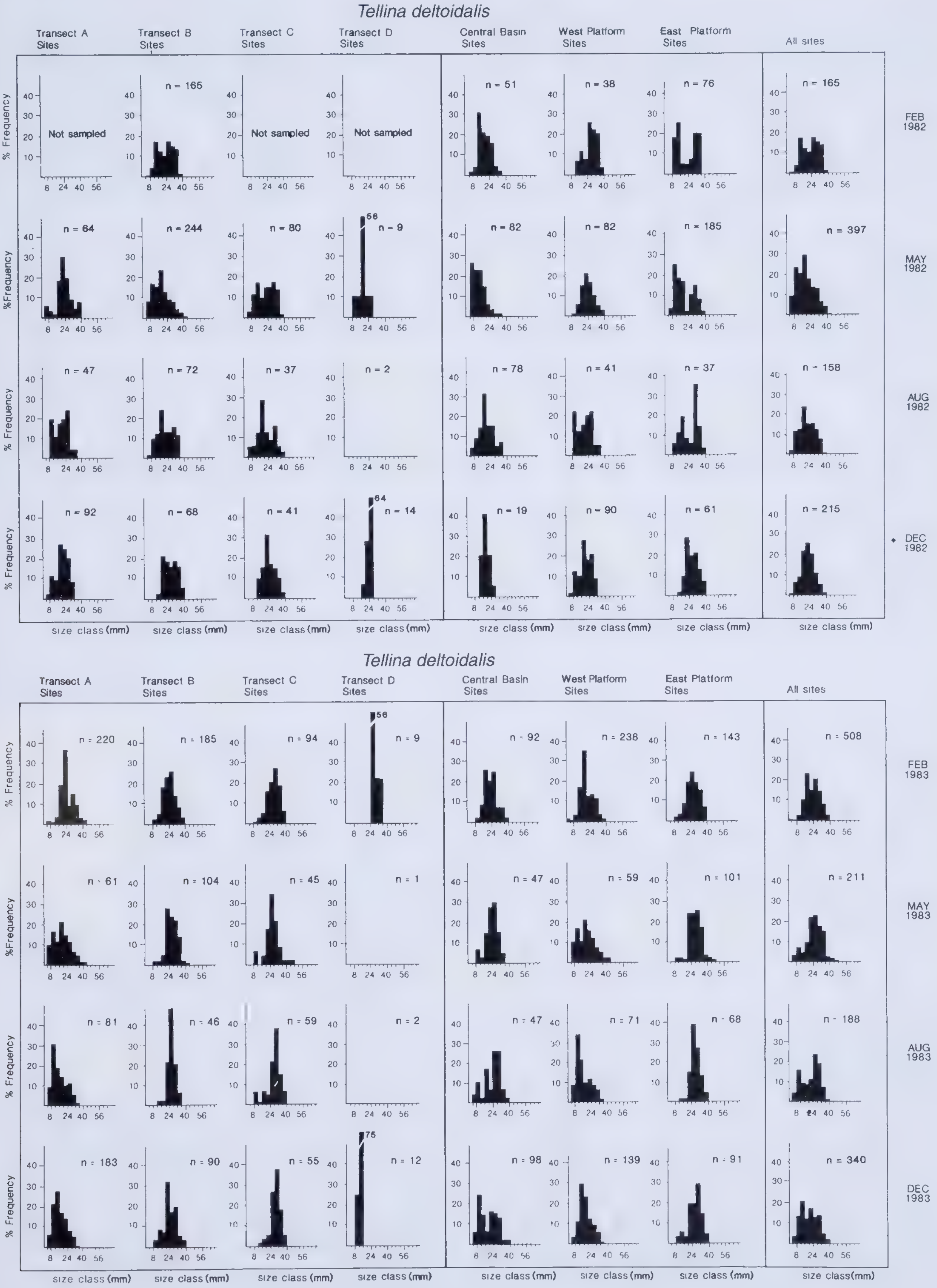

Figure 7. Histograms showing age structure of *Tellina deltoidalis* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where n > 3. Histograms have been constructed where n =3 to n = 20 only to show the size distribution of animals in these very low density populations. A value of n = 0 indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

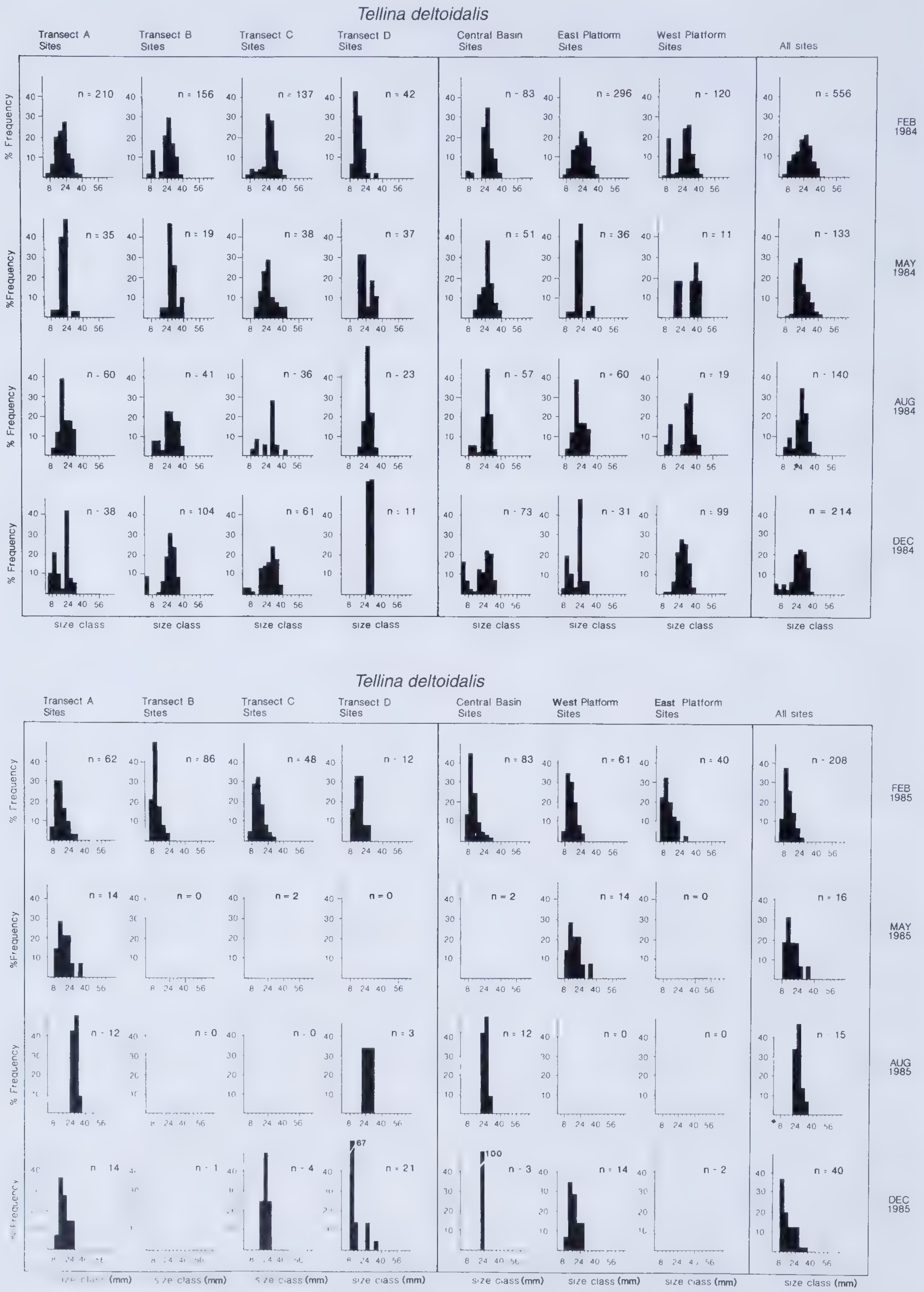

Figure 7 (continued).

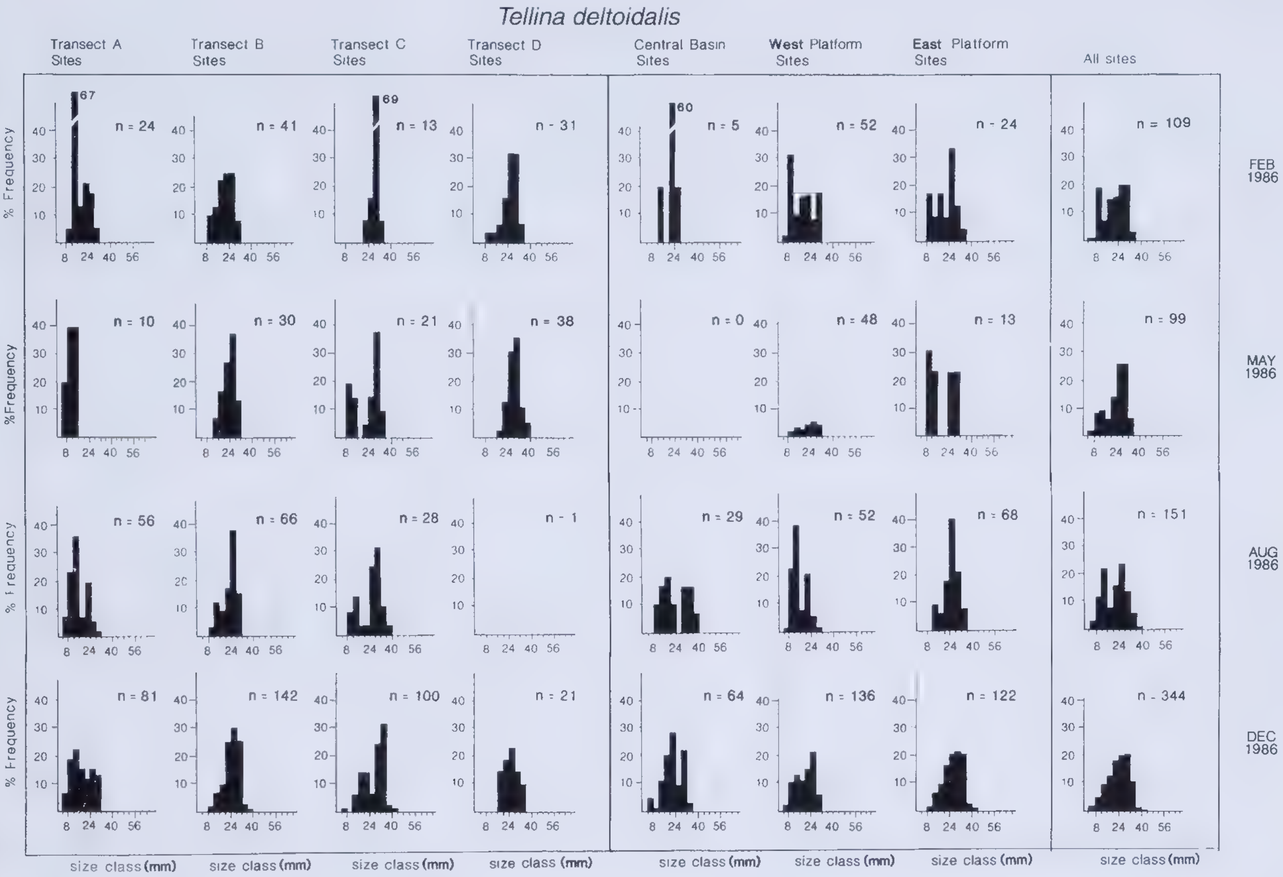

Figure 7 (continued).

deltoidalis was widespread subtidally throughout the estuary. *Bedeva paivae* was relatively widespread subtidally throughout the estuary and in low numbers. *Spisula trigonella* and *Sanguinolaria biradiata* were in low numbers and very scattered in occurrence. *Xenostrobus securis* was restricted to the lower estuary and in low numbers.

Species abundances varied markedly over the course of the study. Even populations of the most abundant and widespread species, such as *A. semen*, *T. deltoidalis* and *N. burchardi*, showed major fluctuations in density within and between sites. In some cases, such as for *T. deltoidalis* and *N. burchardi*, the fluctuations were approximately synchronous. In many cases, population fluctuations appear to have occurred independently of obvious charges in habitat characteristics such as temperature and salinity. For many species, there has been an overall decrease in abundance over the study period such that the relative proportion of species within an assemblage changed over time.

Histograms of size frequency distributions of *Nassarius burchardi*, *Tellina deltoidalis* and *Spisula trigonella* were aggregated in three ways (Figs 7, 9 & 11): from sites along the four monitoring transects, such that population age structures within the various estuarine salinity fields are compared; within large scale habitat sites, *i.e.* the western platform, eastern platform and central basin, such that population age structures between these habitat types determined by substrate/depth are compared; and as an aggregate of all sites for the whole estuary.

Arthritica semen

Arthritica semen was abundant in all salinity fields, typically occurring within 2 cm of the surface, with 100s to 1000s of individuals per square metre (Fig 5 & 15). It was particularly common on tidal sand (A1, A2, A7, B8, C17 and I43), and on tidal and shallow water mud and muddy-sand (M62, M63, J54, J53, K55, L64, F33 and C15). However, the species was periodically quite abundant within the mid-salinity field at C17, a basinal mud site.

The abundance of *A. semen* varied at almost all sites over the study period. At most of sites of its preferred habitat, *A. semen* was present in relatively large numbers during the initial one to two years of the study, after which population density declined. Populations increased again towards the end of 1986 and beginning of 1987. Sites A2, B9, C15, C17 and C19 best show this pattern. At different sites, abundances decreased markedly and variably during the period 1983 to 1987. Population densities also fluctuated abruptly (*e.g.* at C15 from December 1983 to February 1984). These longer term trends do not appear to correlate either with any observed trend in the physical and chemical parameters of the habitat, nor with gradients in habitats occurring across the inlet (*e.g.*, in a given year, *A. semen* was most abundant in summer at C19, D20, and more abundant in winter at A2, A4).

NASSARIIDAE: *Nassarius burchardi*

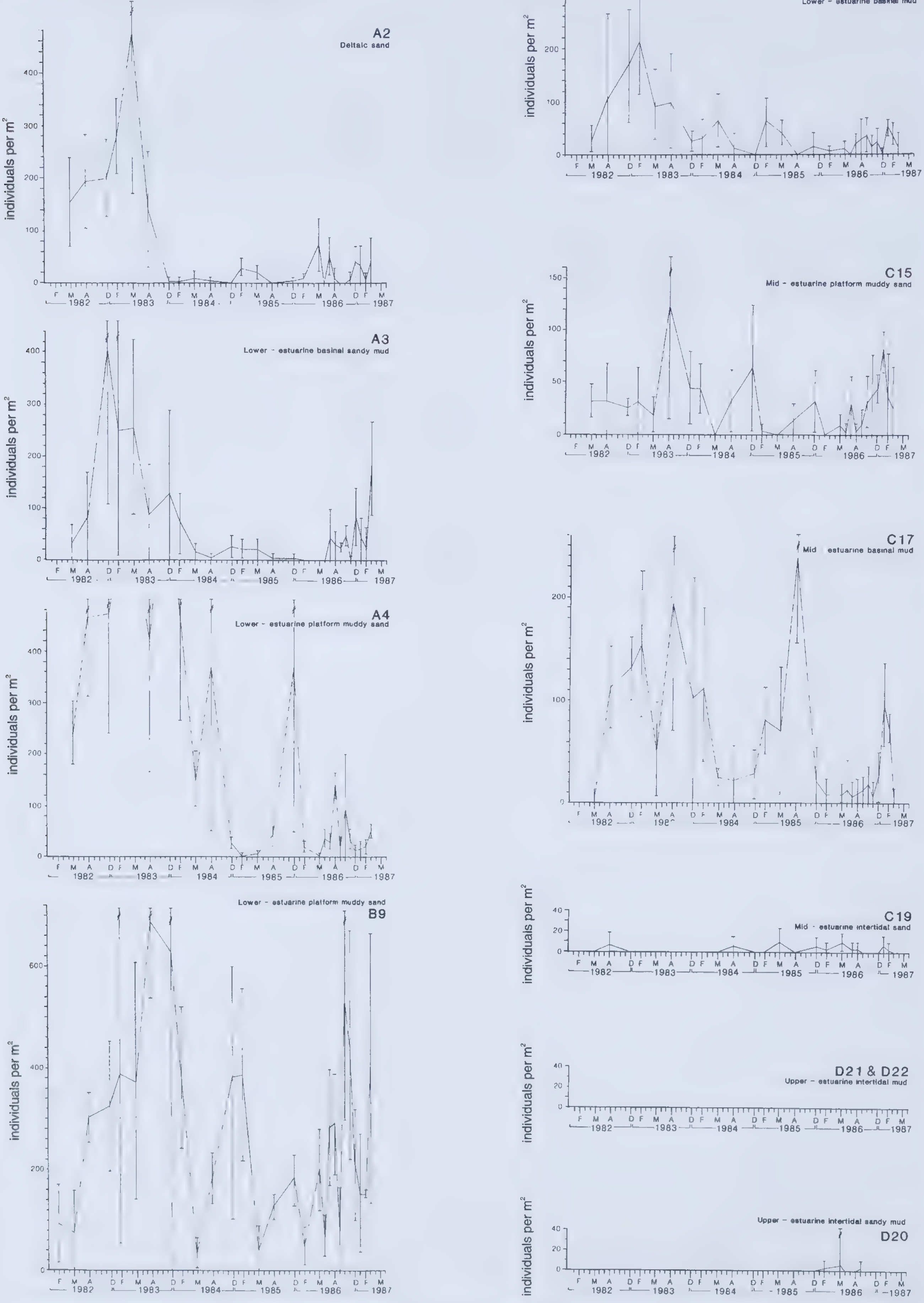

Figure 8. Abundance of individual per m^2 (mean ± sd) for *Nassarius burchardi* at the key sampling sites.

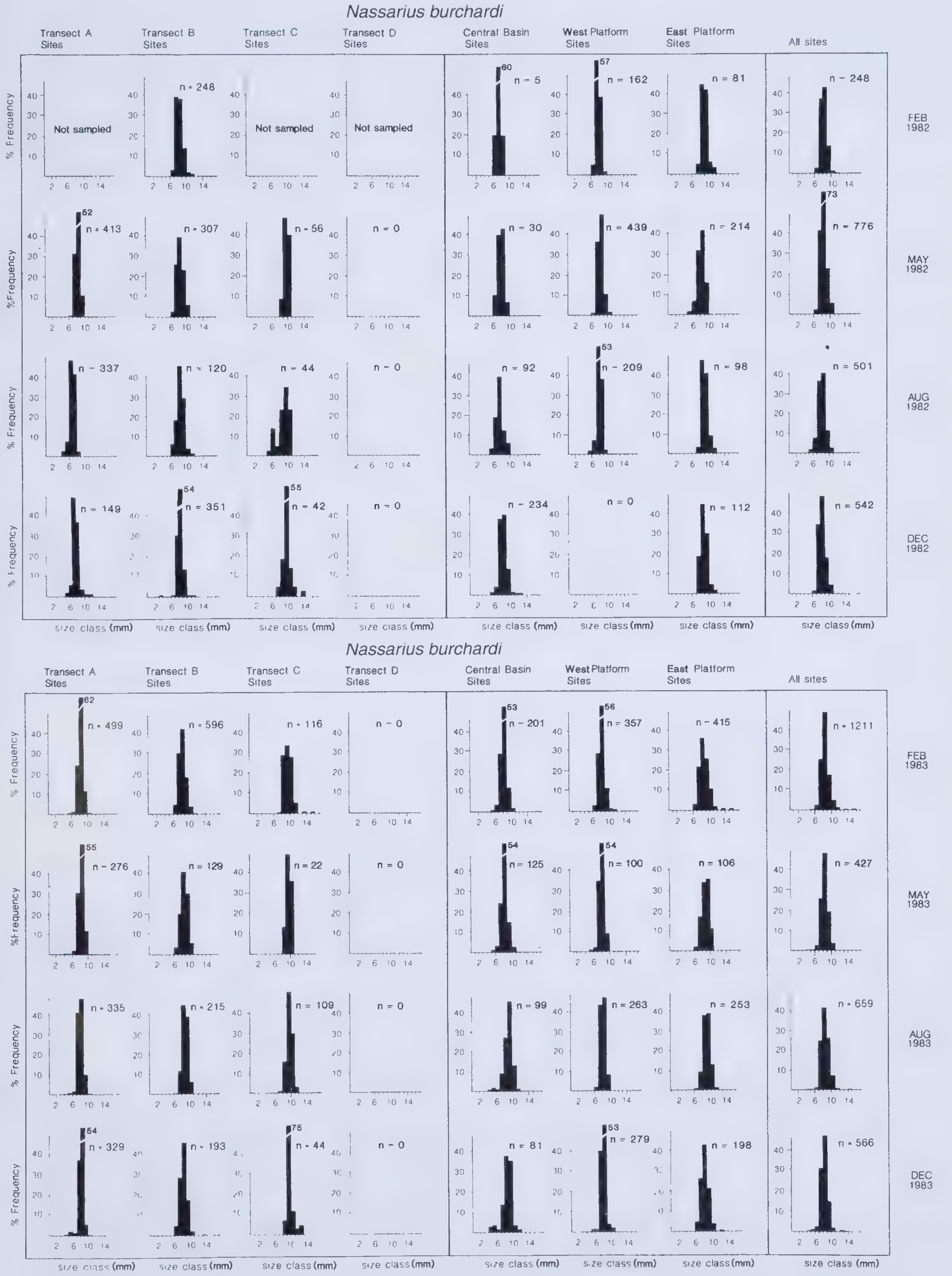

Figure 9. Histograms showing age structure of *Nassarius burchardi* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where n > 3. Histograms have been constructed where n =3 to n = 20 only to show the size distribution of animals in these very low density populations. A value of n = 0 indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

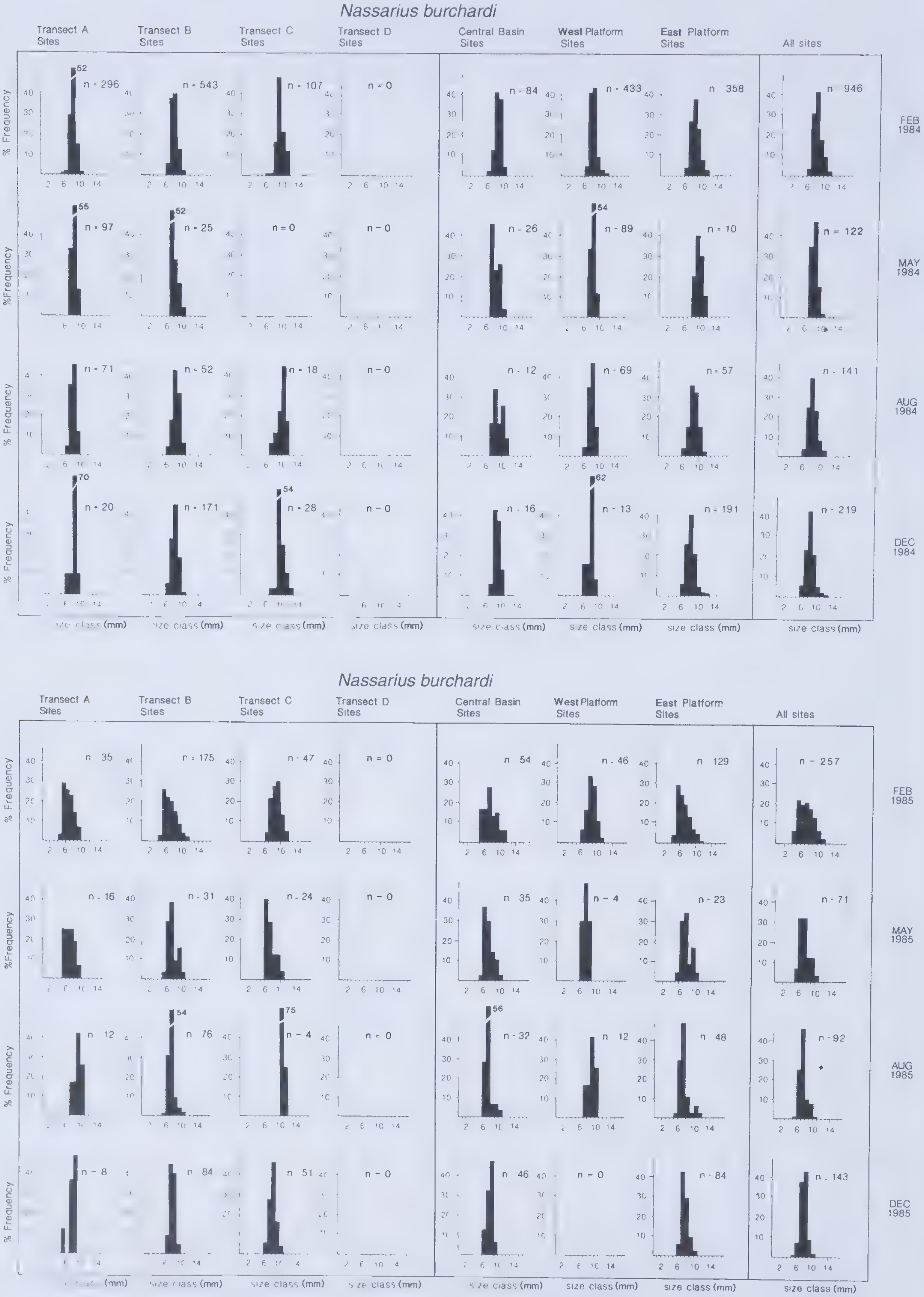

Figure 9 (continued).

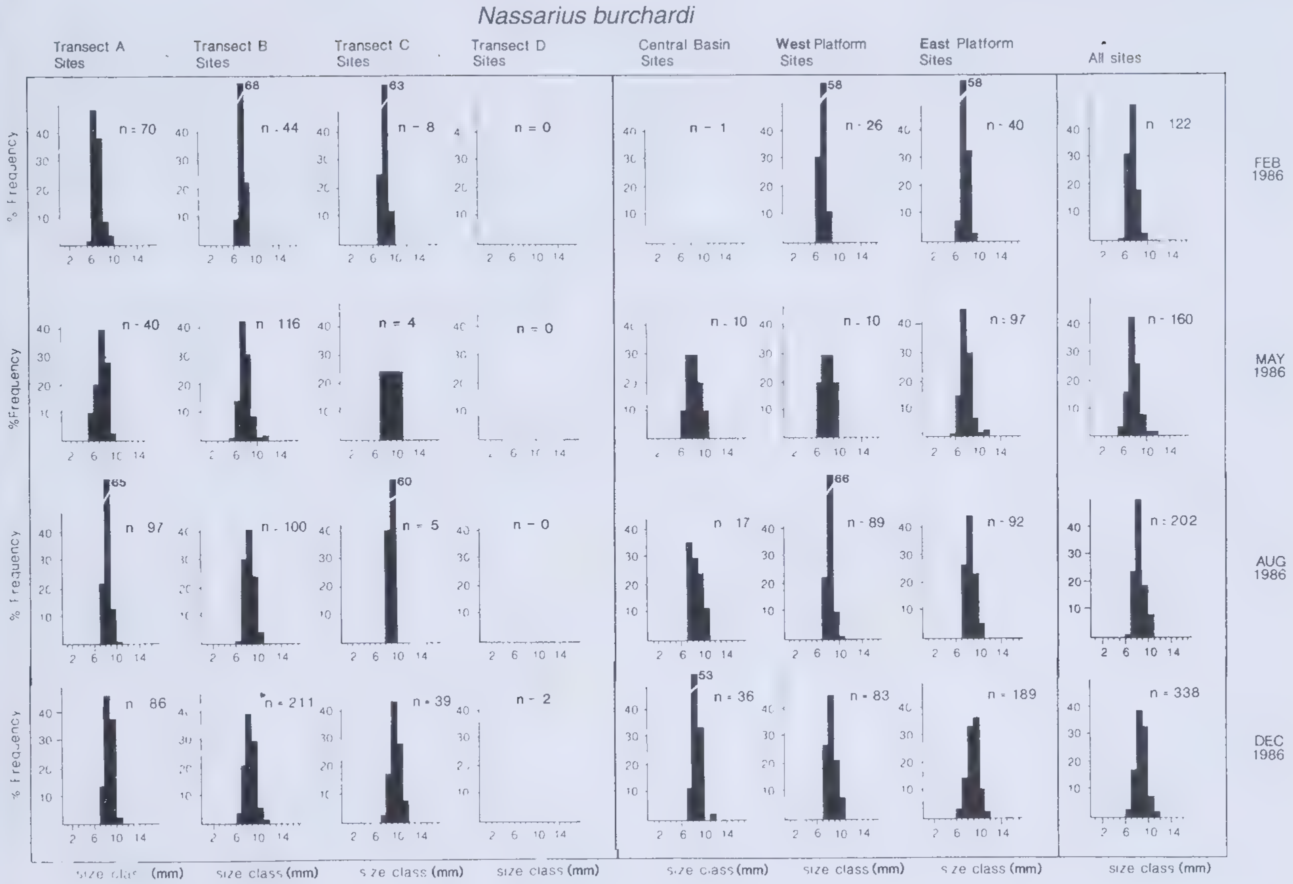

Figure 9 (continued).

Tellina deltoidalis

During the study period, *Tellina deltoidalis* was the most widespread mollusc in Leschenault Inlet, occurring mostly subtidally in almost all substrates, with 10s to 100s of individuals per square meter (Figs 6 & 15). It appears to be euryhaline, occurring in all salinity fields. It was buried to depths of up to at least 25 cm. While inhabiting both muddy and sandy substrates, it was most abundant in vegetated platform muddy-sand sites (A4, A5, E26, J52 and J53), vegetated muddy platform and flat sites (M69, L65, H36, H37, F31, F32), and on some patchily vegetated muddy basinal sites (A3, B11, B12, C17, G35, J49 and K60). Although its relative abundance was lower in habitats of the generally depauperate northern flat, it was, nevertheless, a major component of the fauna of this habitat. The species was rarely found in the coarse deltaic sands, or in sites towards the shoreward edge of tidal slopes (*e.g.* C19, J44, N74, N75, K63, F33 and F42).

Tellina populations exhibit annual cycles of abundance, on lower estuary platform sites (A4 and B9), at a lower estuary basinal site (B11), and at a mid-estuary platform site (C15). Seasonally, numbers reached a peak in late winter to early summer and declined during May with the input of fresh water during winter. Other sites show fluctuations in abundance but not in relation to seasonal patterns. Despite the proximity of some sites, fluctuations in population densities of *T. deltoidalis* did not necessarily correspond. For example, fluctuations in abundance at A3 were not synchronous with those at A4, and abundance patterns at sites along Transect D did not follow the patterns observed along Transects A, B and C. In fact, they exhibited a counter trend to that observed elsewhere with relatively low peaks in abundance in the winter. Along Transcet D, however, sites D21 and D22 had similar fluctuations in population density over the period February 1984 to February 1987.

Histograms of size classes of *T. deltoidalis* show four main patterns (Fig 7): the populations generally were primarily of mature individuals (centred on the 12-30 mm size range); juveniles (arbitrarily defined as < 12 mm long) were consistently present; there had been a continuous low-level of non-seasonal recruitment of juveniles during the study period; and although very small juveniles (*ca* 4 mm size) are generally present in low numbers, they occasionally comprised the majority of individuals at a given site. The size structures, and recruitment patterns were different on the large scale habitats (eastern platform *vs* western platform *vs* central basin), and different in relationship to the gradient in the south to north salinity fields. Three of these patterns are amplified with examples as follows: (1). juvenile recruits were found at sites along Transect A between May 1982 and December 1982, at sites along Transect C between May 1983 and August 1983, and at those along western platform between February 1984 and December 1984; (2). there was a change in population structure, with differing sizes and differing proportions of adults and juveniles from east to west across the estuary, as exemplified by the sites within the central basin, those

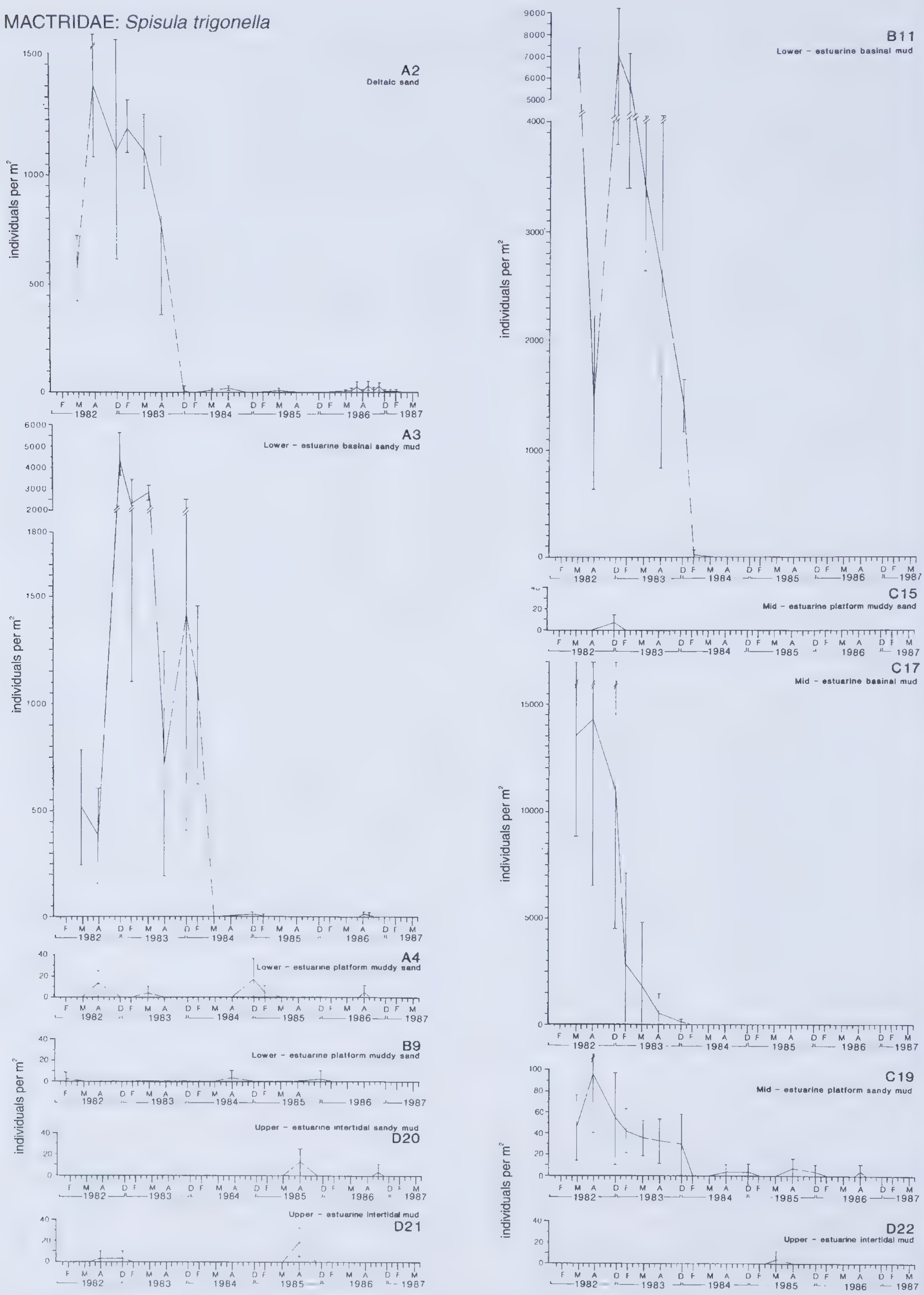

Figure 10. Abundance of individual per m² (mean ± sd) for *Spisula trigonella* at the key monitoring sites.

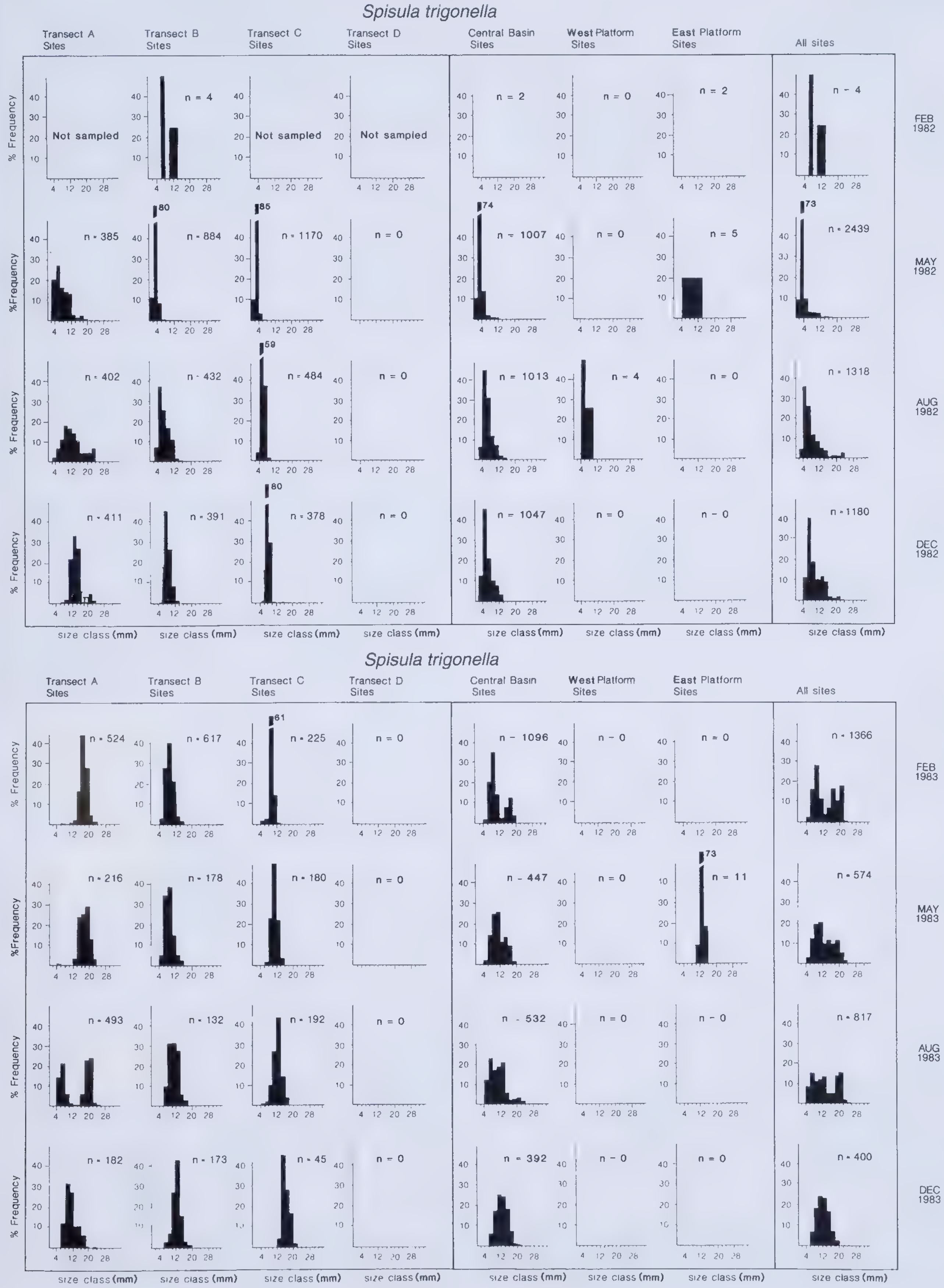

Figure 11. Histograms showing age structure of *Spisula trigonella* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where n > 3. Histograms have been constructed where n =3 to n = 20 only to show the size distribution of animals in these very low density populations. A value of n = 0 indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

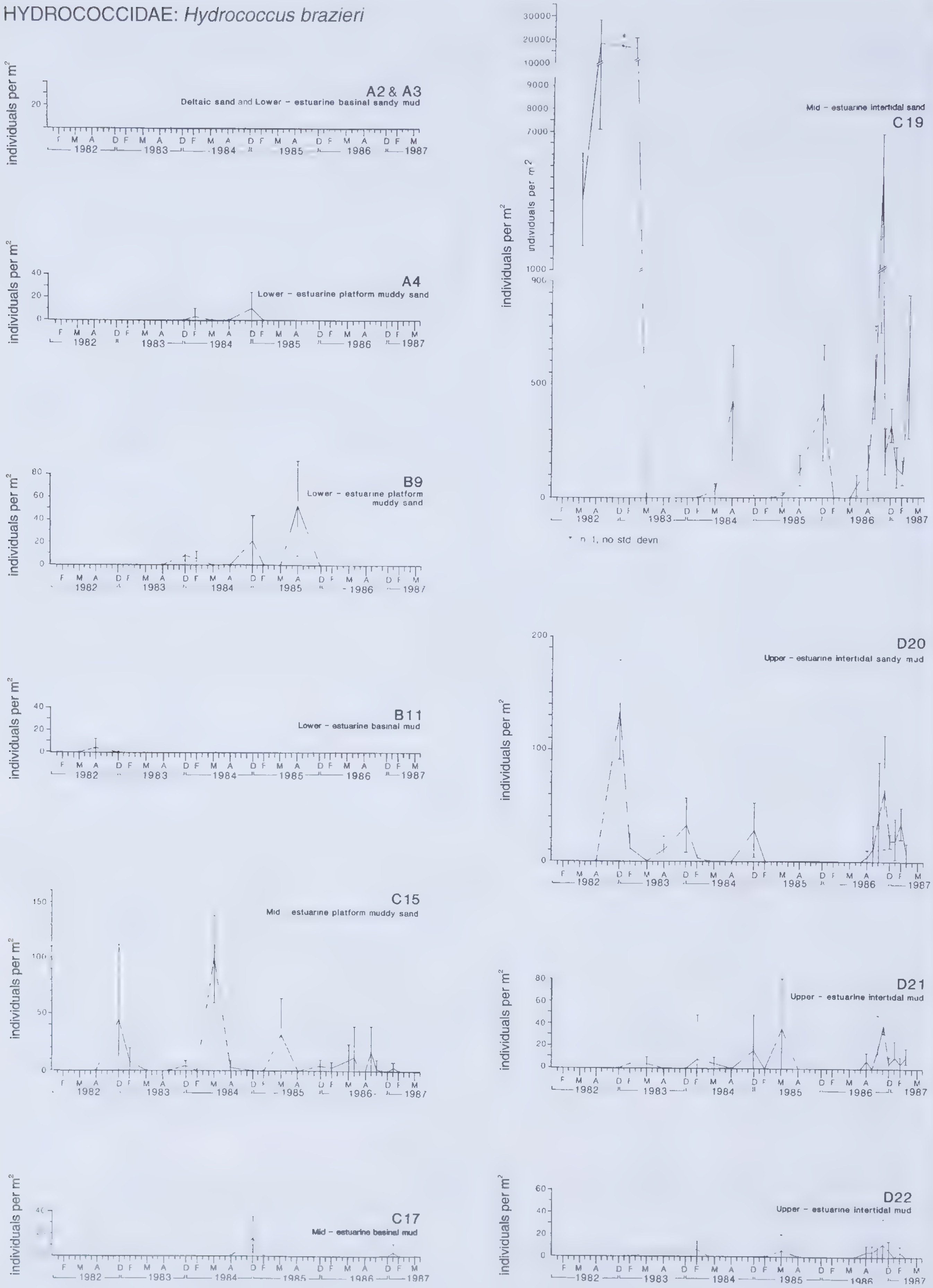

Figure 12. Abundance of individual per m² (mean ± sd) for *Hydrococcus brazieri* at the key monitoring sites.

SCAPHANDRIDAE: *Acteocina* sp.

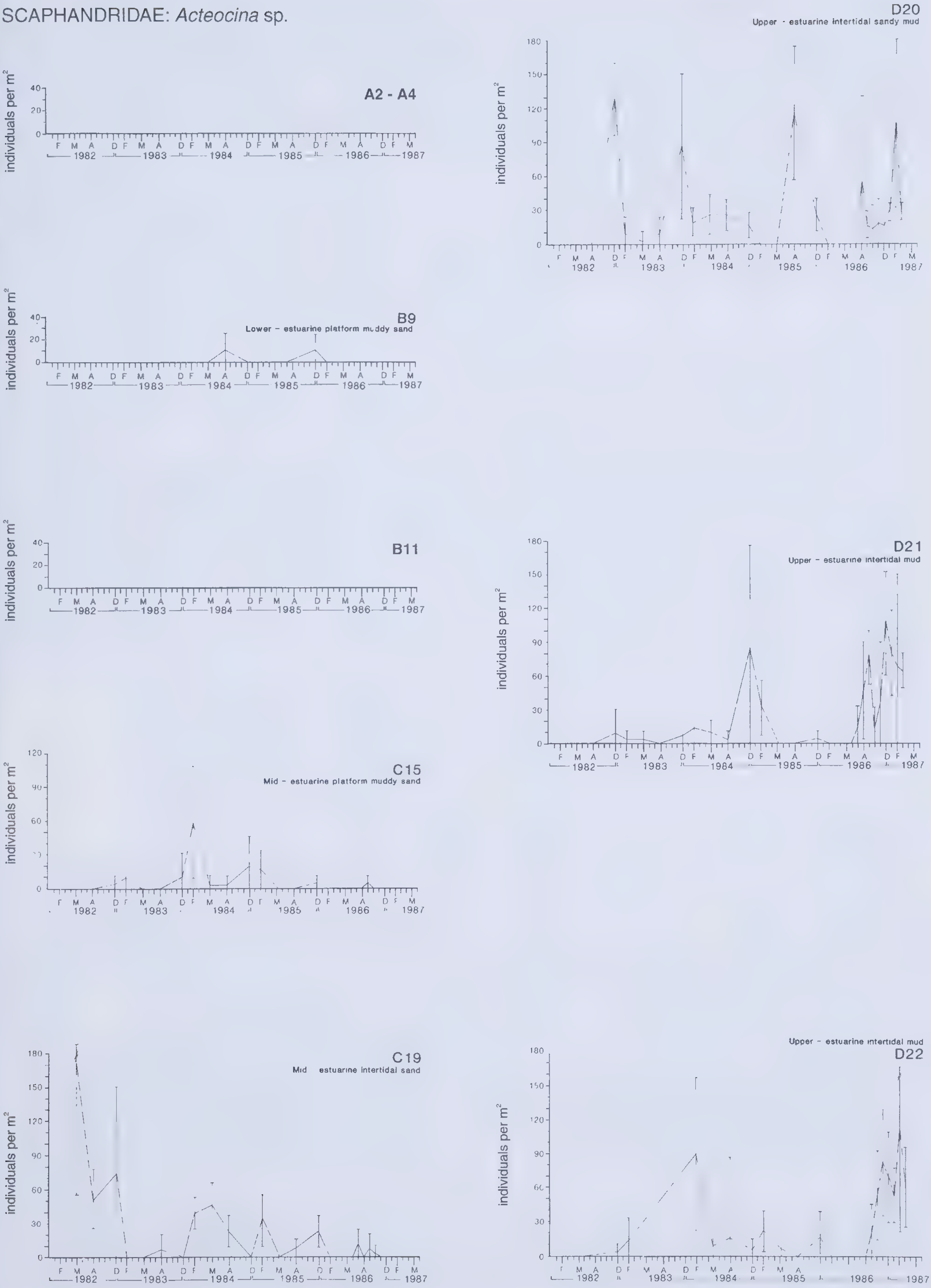

Figure 13. Abundance of individual per m^2 (mean ± sd) for *Acteocina* at the key monitoring sites.

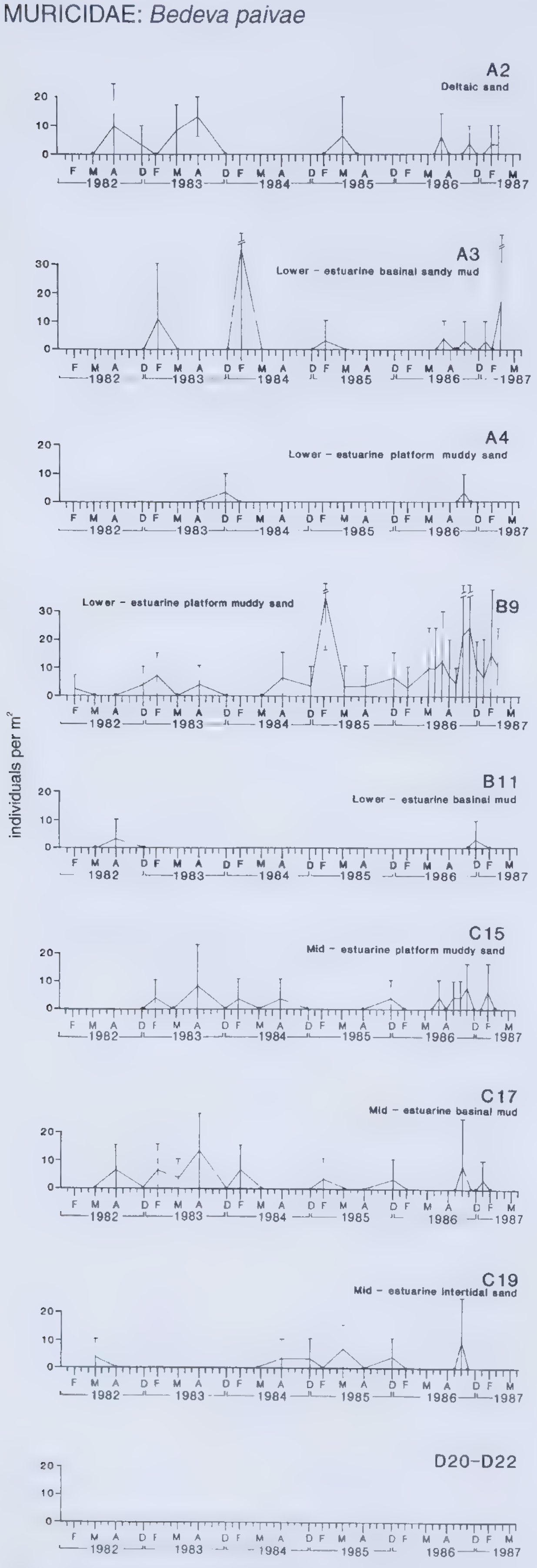

Figure 14. Abundance of individual per m^2 (mean ± sd) for *Bedeva paivae* at the key monitoring sites.

along the western platform, and sites along the eastern platform for May and August 1982, and for August to December 1983; and (3). there was a progressive growth trend and a shift of the mode of the histogram over the year, as exemplified by sites along the eastern platform between February 1982 and February 1983, those along Transect C between February 1983 and February 1984, and all sites between May 1982 and May 1983.

Using age structure histograms from May 1982 to December 1982 to trace the progressive growth of juveniles over 7 months, and commencing with a clearly bimodal population of adults and recently recruited juveniles present in May 1982, *T. deltoidalis* appeared to have had a growth of *ca* 12 mm over that period, giving an average growth of 1.7 mm per month.

Nassarius burchardi

Nassarius burchardi was common throughout all subtidal habitats, and was consistently present during the study period (Figs 8 & 15). It was most abundant at vegetated sites on eastern and western platforms, occurring in 100s per metre square and was generally absent, or much less abundant, on substrates within the upper estuarine salinity field. There was a decrease in numbers of individuals within the estuary after the first two years of the study (*e.g.* A2, A3, A4, B10, B11 and B12).

Fluctuations in population density of the species were broadly similar for sites A2, A3, A4, B9, B11 and C17, albeit that the patterns were magnified at sites A4 and B9, and the timing of the peaks of abundance were not exactly in phase. At these sites, *N. burchardi* populations were dense over the period 1982-1983, declined in adundance thereafter, then increased slightly for a short period for part of 1985, and then increased over the period mid-1986 to mid-1987. There was some synchronicity in patterns of abundance for sites A2, A3, A4 and B11.

In this study, *N. burchardi* was more abundant at A4, on well vegetated muddy-sand on the western platform, than at any other site in the estuary. On deltaic sand (A2), the species was most abundant during early 1983; numbers then decreased abruptly after December 1983, and remained low throughout 1984 and 1985. This decline corresponded with a major fresh water influx (< 5 ‰ salinity at A3) during August 1983 (*cf* Kowarsky 1969; Smith 1975). Along Transect B there was a net decline in abundance from 1982 at all sites except B9 and B14. These latter sites showed reduced numbers during mid 1985 to mid 1986. Along Transect B, the species was most abundant at B9 (a vegetated platform sand habitat). The long-term population densities of the species here were largely maintained, apart from declines in abundance during May in 1984 and 1985. Trends in variation in abundance, however, were not ubiquitous, *e.g.* there was no net decrease in abundance at B8, B9 and B14, while concurrently there was marked decline in abundance at B10, B11, B12 and B13. Along Transect C, *N. burchardi* was most abundant at C15, C16 and C17, but generally less abundant than at sites along Transect B. At C15 and C17, there was some cyclicity to the fluctuations in its abundance, with a decline in numbers occurring during late summer to winter. Overall, there appeared to be a decrease in

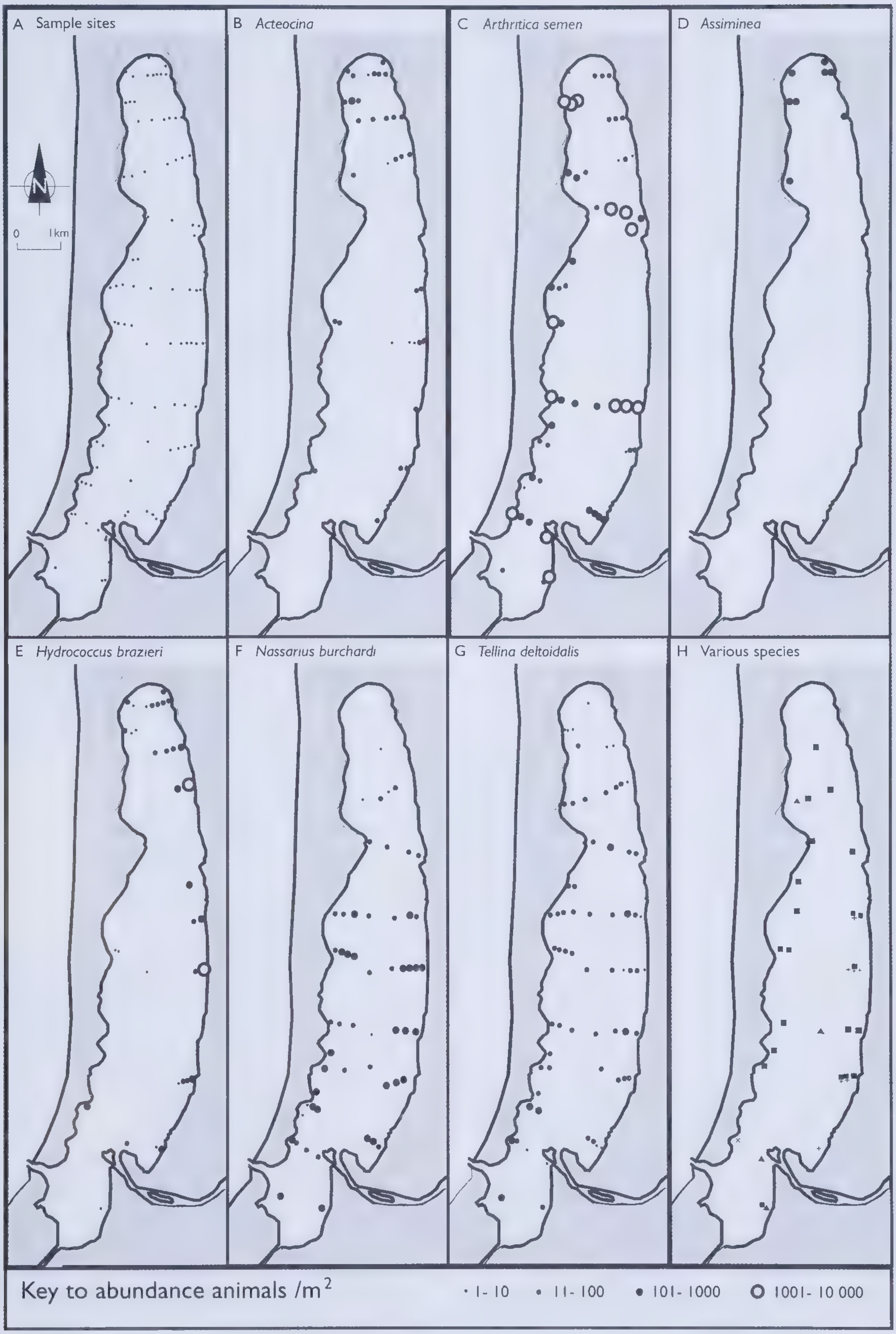

Figure 15. Distribution and relative abundance of key mollusc species in December 1986 (data from Wurm 1987). **A:** Sampling sites. **B-G:** Abundance of animals for a given species. Size of circle reflects relative abundance of animals based on three replicate samples. No symbol at a sampling site denotes zero animals. **H:** Occurrence of various other species, with local population density for each species < 10 / m^2 (see Appendix 1 for details): *Bedeva paivae* (black square), *Sanguinolaria biradiata* (+), *Spisula trigonella* (black triangle), and *Xenostrobus securis* (x)

abundance of *N. burchardi*, relative declines in abundance in late summer to early winter, with peaks in abundance in late winter/summer, major fluctuations in abundance at some sites that did not correlate with extremes of salinity and temperature, and cyclicity in abundances.

Histograms of size classes for *N. burchardi* for the various sites show a fairly uniform pattern of unimodal populations, with a mode centred on the 8 mm size class for most of the years of sampling (Fig 9). This mode occurred within all salinity fields and at all sites on all large scale habitats, indicating no growth, and persistence over several years of individuals in the population. Occasionally, there was a minor mode due to the recruitment of juveniles, such as in August 1982 in sites along Transect C, and in August and December 1983 and December 1985 in sites of the central basin and along Transect A, and in September 1986 along Transect A.

Spisula trigonella

Spisula trigonella was very abundant at many sites at the beginning of the study, being most abundant in the basinal mud of the mid and lower estuary, with 1000s of individuals per square metre (Fig 10). *S. trigonella* was also abundant on the tidal and subtidal coarse sands of the Collie River delta system and in the mid tidal sand at C15. It was found only rarely on vegetated sites on the eastern and western platform, and in the upper estuarine salinity field of the northern flat. During the study, its overall abundance in the estuary dropped markedly, such that by 1987 it was uncommon to absent in all habitats.

Along Transect A, *S. trigonella* was most abundant in deltaic sand at site A2, and in basinal sandy-mud at site A3 in the lower estuary. Peak abundance occurred in May 1982. Numbers began to decline by August 1983 and the species was absent by December 1983. At A3, the peak of abundance was not reached until December 1982, three months later than at A2, and numbers declined by August 1983. Maximum decline in numbers did not occur until after February 1984, due to further recruitment of juveniles at the site. By May 1984, *S. trigonella* was almost entirely absent at this site also. At B11, there appeared to be two peaks in abundance, one in May 1982, the other from December 1982 to February 1983. These do not correlate with any observed pattern of juvenile recruitment and may be due to sampling of the spatial variability in animal density. The species was absent at site B11 by February 1984. Along Transect C, *S. trigonella* was most abundant at C17, a mid estuarine basinal mud site. It was more abundant here than elsewhere in the inlet. It also was relatively abundant at C19 on the mid estuarine tidal sand. Elsewhere in the estuary it was generally absent or uncommon on subtidal platform and tidal environments. A similar abrupt decline in abundance began after December 1982 at sites along Transect C and was complete by December 1983, almost a year earlier than at Transects A and B. Along Transect D, *S. trigonella* was most absent. Three patterns, however, are evident: the major recruitment in the lower to middle estuary is reflected in a small population at site D21; small populations of the species appear in May-August 1985, synchronous with site C19; and a small population appears at site D20 between August and December 1986, synchronous with some sites along Transect A.

Histograms of size classes for the species show the patterns of recruitment, and varying growth rates, depending on setting according to large scale habitats and in relation to the south to north gradient in salinity fields (Fig 11). Population structures are variable from eastern platform to western platform to central basin, depending on whether juvenile recruitment had occurred in the given habitat There was a major juvenile recruitment mainly located in the central basin along all transects in May 1982. Following this, there was a progressive shift in the size mode of the population through time. By December 1982, the populations along all transects were numerically dominated by the age cohort arising from this single recruitment event. There also appeared to have been a smaller recruitment in August 1983 in the region of Transect A, and a possibly a small recruitment in the period between August and December 1985.

The size histograms for 1982 indicate growth rates of *S. trigonella* individuals along all three transects initially to be *ca* 0.6 mm per month. A difference in growth rate from south to north (Transect A to Transect C) is evident during 1982 and 1983. By December 1983, the numerically dominant age cohort, arising as juveniles at sites along Transect A in May 1982, was predominantly in the 18 to 22 mm range. However, the cohort along Transect B at the same time was 8-14 mm in size, and that along Transect C was 10-14 mm in size. The total population for the inlet in February 1983 showed a bimodal population structure. Traditionally, assessment of the total population from many sites in an estuary is often undertaken by researchers to determine regional population structures and recruitment patterns, and it is in this sense only that the total population was used, to highlight the invalidity of such an approach. The temporal sequence of histograms for *S. trigonella* in the estuary indicates there had been no further recruitment in the estuary, and that the bimodal size structure was due to the rates of growth of animals at Transect C differing from those at the other transects to the south. By May 1983, the two modes began to merge. In August 1983, the population of the estuary was again bimodal, due to the arrival of another cohort of juveniles only at Transect A. This influx of recruits this time is not clearly reflected in the abundance graphs. This latter cohort maintained the presence of *S. trigonella* at A3 into early 1984.

Six individuals of *S. trigonella*, 12-18 mm in size, were recorded along Transect D, in the upper estuarine salinity field, during August 1985. These were obtained from widespread sampling at site D22 (sampling continued until 40 box cores were obtained to ensure that determination of population density was valid). The results indicated that the population was of very low density, and consisted of residual adults. The size range of *S. trigonella* at this time corresponded to an age of approximately one year, based on interpreted growth rates along Transect C. However, the growth rate of individuals was probably even slower along Transect D. Some juveniles, 6 mm in size, were recorded at Transect A in February/May 1985 and in August 1986, indicating that there was some low level recruitment, although not at the scale of the major recruitment event in May 1982.

Hydrococcus brazieri

Hydrococcus brazieri occurred on, or was buried shallowly within substrates, particularly those on tidally exposed surfaces, but also locally on shallow subtidal sites (Figs 12 & 15). The species inhabited specific sites intermittently during the study period, occasionally increasing in abundance to 10s or 100s of individuals per square metre. It was most abundant in mid and upper estuarine salinity fields on tidal sand and muddy-sand (*e.g.* C19, N74, M73, J44, K63 and F27) but also inhabited some platform muddy-sand (*e.g.* C15, M72 and J45), and tidal mud in the upper estuarine salinity fields (*e.g.* D20, D21, D22, O85, O80, N76 and N77). In these latter habitats, it was less abundant and was not consistently present.

H. brazieri was most abundant at a mid estuarine tidal sand site (C19) and its occurrence there is described in detail to illustrate the dynamics in the population. Seasonal peaks in abundance occurred in winter or summer, and there was a consistent annual decline in population numbers during February and May. Overall, there was a general decrease in abundance of the species from a record of 1000s per square metre in 1982. Subsequently, the species was not recorded there between February 1983 and May 1984, and may have been eliminated between January and May 1983 as a result of high salinities (up to 45 ‰), coupled with high summer water temperatures. A search along the strand in the proximal vicinity of C19, to locate another populations, failed to find the species. Similar salinities during summer 1986/87 did not eliminate the species from the site C19, although numbers had decreased, but at this time the temperatures of the water, and of the air where the site was exposed, were lower than those during the 1983 period of high salinity.

At A7, between 1982 and 1985, the species was absent, but made its first appearance in winter 1986, steadily increasing in abundance up to summer 1987. Site A7, located at the distal edge of the Collie River delta, had been naturally modified in late 1985 by an incursion of a sheet of deltaic sand, which built the surface to a higher tidal level. This species progressively colonized the newly accreted surface. At C15, a mid estuary platform muddy-sand site, the abundance of the species varied over five years, with annual peaks occurring generally in mid- to late summer. However these were much lower than at C19. Similarly, at upper estuarine tidal sandy-mud and mud sites (D20, D21, and D22), its abundance varied over the study period, peaking generally in mid to late summer. Sites D21 and D22 appear to show sympathetic fluctuations in population density over the period February 1984 to February 1987.

Acteocina sp

Acteocina sp was most abundant in tidal mud in the upper estuarine salinity fields of the northern flat (*e.g.* at D20 and D21), forming populations of several to 10s to 100s of individuals per square metre (Figs 13 & 15). It also inhabited tidal sand (*e.g.* at C19, B8, H42 and F27). *Acteocina* was most consistently present at C15, C19, D20, D21 and D22. Its abundance fluctuated, generally being more abundant during summer, although locally reaching peak abundance at some sites in winter or autumn. At C19, there was a nett decrease in abundance over the study period, with peaks in abundance occurring during late summer to winter. At C15, although *Acteocina* was in relatively low numbers, there was a general increase in abundance in summer.

Other less abundant species

Species which were present throughout the study period, but in low numbers, included *Assiminea* sp, *Bedeva paivae*, and *Sanguinolaria biradiata* (Fig 15). While overall *Assiminea* sp was not common in this study, in general it was consistently present in low numbers, mostly inhabiting tidal to shallow water sandy-mud and mud habitats along Transect D, and sites O87, O86, O85, O80, N74 and M66 in the upper estuary. The most southerly occurrence of the species was on shallow vegetated muddy-sand at C15. *Bedeva paivae* occurred in many habitat types, generally in low abundance (Figs 14 & 15). It mostly inhabited platform sites B9 and B10. Locally, it inhabited upper estuarine habitats (*e.g.* N77, M68 and M69). There was a continued presence in the estuary during the study period, with no correlation in fluctuations in abundance and measured environmental parameters. A localized population of *Xenostrobus securis* became established in coarse sands of the Collie River delta in August 1982. It increased in density the following summer, reaching a peak in abundance when surrounding salinity approximated sea water, and when the water temperature would have been high (*ca* 25-28 °C). The population was absent by August 1983. Other populations were found at A4 in December 1983 and A5 in December 1986. *Sanguinolaria biradiata* was present throughout the study period and across much of the estuary, but in low numbers, occurring most commonly on peripheral sand or muddy-sand substrates in the mid estuarine and lower estuarine salinity fields.

Discussion

Habitat type and mollusc distribution

The dynamic and varied nature of the Leschenault Inlet estuary has produced complex responses of the biota, in the patterns of abundance and population maintenance, and although most of the more abundant species occurred at least rarely in most habitat types, the relative abundance of a given species clearly corresponded with a habitat type(s) and substrate (Table 4). For example, *A. semen* and *H. brazieri* were predominantly tidal-substrate inhabitants in all salinity fields. *S. trigonella,* when abundant in the estuary, occurred selectively on substrate types which were unvegetated in the mid estuarine, lower estuarine, and deltaic salinity fields. *B. paivae* occurred in all salinity fields, predominantly on shallow water platform substrates, rather than on deep water basinal or tidal substrates (notably, *B. paivae* normally is found on hard substrates, but in Leschenault Inlet estuary it inhabits sandy and muddy sand substrates). *Tellina deltoidalis,* although common in all subtidal habitat types, occurred most abundantly in well vegetated platform substrates in the mid and lower estuarine salinity fields. *Nassarius burchardi* also was common in all subtidal habitats, being most abundant in well vegetated platform habitats in the mid and lower estuarine salinity fields. *Sanguinolaria biradiata* occurred most commonly on peripheral sand or muddy-sand substrates in the mid estuarine and lower estuarine salinity fields. Ultimately the distribution of a particular species may be determined by smaller scale phenomena which may occur within those units identified at the large scale, however, species distribution may also transcend identified habitat boundaries, or occur as zones or mosaics within them.

Salinity and temperature generally are important factors limiting mollusc distribution. Salinities of 60 ‰ and temperatures of up to 32 °C occur in summer in the upper estuarine salinity field, and these would be limiting for even the truly estuarine species *A. semen* and *H. brazieri* (Wells & Threlfall 1982a). Elsewhere in the estuary, the range of salinities and water temperatures begin to delineate mollusc assemblages of marine affinity at one extreme, and those of truly estuary character at the other. Oxygen concentrations rarely fell below 6 mg L^{-1} during this study, and thus does not appear to be a limiting factor. Even so, estuarine fauna are known to adapt to low oxygen tensions and cope with dynamic estuarine through an ability to conform their consumption to ambient oxygen levels or to rest during low oxygen concentrations (*e.g.* Hammen 1976).

The main distribution over the medium term of the key mollusc species with respect to bathymetry and habitat, and in relation to the estuarine hydrochemical field in the Leschenault Inlet estuary is summarised in Fig 16. Mixed mollusc assemblage occurred in the basin environment and *X. securis* occurred in shallow water, both in the lower estuary. *Acteocina* was restricted to the tidal and shallow tidal habitats mainly in the upper estuary. *H. brazieri* and *A. semen* were located mainly in tidal habitats throughout the estuary. *T. deltoidalis* and *N. burchardi* were widespread throughout the estuary, occurring in nearly all habitats. *B. paivae* was present on shallow water platforms in middle to lower estuary, and in the shallow water subtidal of the upper estuary. *S. biradiata* was mainly restricted to the eastern platform and intertidal of the middle estuary. *S. trigonella*, when it was abundant, inhabited the basin of the middle estuary and the basin of the lower estuary and shallow water to tidal zone of the delta.

Abundance and population dynamics

This study provides a perspective of changes in mollusc abundance over 5 years in the Leschenault Inlet estuary and an insight into their variability and longevity. For instance, some species have been consistently present, although abundances varied seasonally, whereas the presence of others fluctuated markedly. While the overall character of the mollusc assemblages in the estuary over the study period remained similar, there also have been significant changes from year to year, and from season to season. Despite the medium term nature of this study, the reasons behind the patterns of abundance in populations of the molluscs were not readily identified. In most cases, the abundances of a given species fluctuated independently of others, and for many species did not appear to directly relate to seasonal patterns in salinity, temperature, or oxygen concentration. For some short-lived species, the timing of peaks in abundance occurring after a decline in population density may be determined by the rate of the extra estuarine recruitment of juveniles, which may not necessarily directly correlate with ideal environmental conditions in the estuary. Some of the variation in abundance in time may be an artifact of sampling patchy populations.

Population structures and their temporal variation were different for the three species investigated. *Spisula* was numerically dominated by one age cohort which progressed in time from juveniles to adults, and was not maintained significantly by further recruitment. *Tellina* appeared to be maintained by a relatively continuous low level of juvenile recruitment, and *Nassarius* was dominated by a persistent mature age cohort, with an intermittent low level of juvenile recruitment which did not maintain the size of the population at its initial level.

Population structures for a given species were also different in relation to habitats, *viz.* recruitment patterns could be different from western to eastern platforms, from the central basins to the shallow water platforms, in response to the south to north salinity fields, and even within the one habitat setting, from site to site. This indicates that there are significant intra-estuarine determining factors that can regulate the population dynamics of mollusc species on a habitat to habitat basis, and within a habitat, on a site to site basis. As such, it is clear that recruitment patterns and population maintenance patterns are not similar estuary-wide.

In summary, the interpretations and discussion that follow suggest that the various mollusc species are responding independently and in different ways to the varied estuarine environment. The mollusc fauna was comprised of a group of species sharing a common habitat but differing in their life strategies and population maintenance mechanisms (*e.g.*, of a range of species cohabiting the same environment: *Bedeva* is a carnivore, *Tellina* is a detrital feeder, *Nassarius* is a scavenger; *cf* Morton & Britton 1991), a factor noted by Wells & Threlfall (1981). Although the distribution of a particular species was correlated with one or more habitat types, the size of the population of a given species, with time, varied markedly within habitats. Consequently, for a realistic indication of the presence and relative abundance of each species in a given assemblage or habitat, populations or habitats must be sampled through time at least over the medium term. For the more common mollusc species, patterns of distribution, abundance, and population dynamics, and summary of the literature on their autecology as it relates to Leschenault Inlet are discussed below.

Arthritica semen

In the Leschenault Inlet estuary, *A. semen* was abundant in all salinity fields, particularly in tidal mud and sandy-mud substrates. Its abundance varied over 5 years, from a peak early in the study, to low levels shortly thereafter, to an increased abundance late in the study. The species appeared tolerant of high salinities and temperatures, and patterns in its abundance did not correlate with extremes in water parameters. Clearly some other factors had influenced its abundance. Natural patchiness could be one

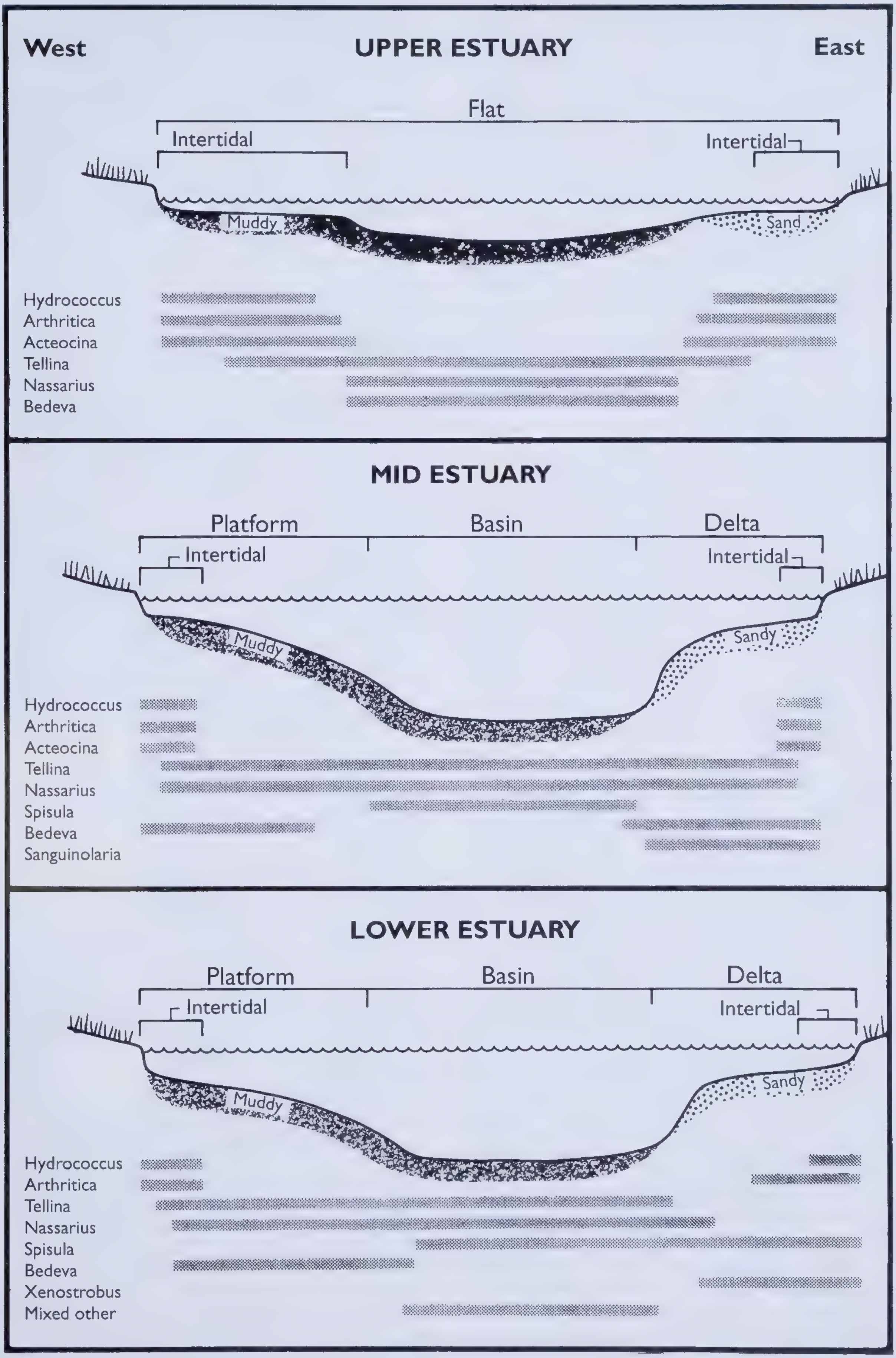

Figure 16. Summary schematic illustration showing the main molluscs and their distribution across the main habitats from lower estuary to upper estuary.

explanation, predation could be another. Fish, for example, are known to prey on small molluscs (Potter *et al.* 2000).

Studies of reproduction over two years in the nearby Peel-Harvey estuary system by Wells & Threlfall (1982b) showed no seasonality in breeding, with animals in the field reproducing almost continuously. The number of females brooding and the number of juveniles varied between months with no seasonal correlation. Larvae were found to undergo several developmental stages in the brood pouch, and shelled juveniles are released directly from the female, with individuals reaching maturity after 6 months and maximum size in 9 months, with a probability some animals surviving for a second year (Wells *et al.* 1980; Wells & Threlfall 1982c). This is relevant to the situation at Leschenault Inlet, as it explains the ever-present large numbers of individuals within the populations.

A. semen occurs elsewhere in south-western Australian estuaries, from Albany to Moore River. Information useful to interpreting the population dynamics of the species in the Leschenault Inlet estuary is provided by such studies elsewhere. For example, the species is abundant on shallow-water sand flats in the Swan River Estuary (Ashman *et al.* 1969; Chalmer *et al.* 1976) and in the Peel-Harvey Estuary (in densities up to thousands m^{-2}; Wells & Threlfall 1982c). During monthly monitoring over 2 years in the Peel-Harvey Estuary, the density of individuals varied markedly from month to month with no apparent correlation with season. Changes in abundances were abrupt, with numbers of individuals dropping from 45 491 m^{-2} to 4 893 m^{-2} in several months (Wells & Threlfall 1982c). In laboratory experiments, *A. semen* tolerated a wide range of temperatures and salinities (Ashman *et al.* 1969; Wells & Threlfall 1982a), remaining active between 18 °C and 32 °C, and at salinities of 10 ‰ to 54 ‰, though the effects of high temperature and high salinity act synergystically to cause inactivity. The species was also able to survive salinities < 10 ‰ and a median lethal temperature of 37 °C, simulating the extremes in winter and summer conditions. These results corroborate and help explain the patterns of the population dynamics of the species in the Leschenault Inlet estuary.

Tellina deltoidalis

Tellina deltoidalis was widespread in the estuary in all subtidal habitats except that of the Collie River delta. It was less abundant in the upper estuarine salinity field but was still a dominant component of the low intertidal and subtidal habitats there. The species was most abundant in vegetated muddy substrates of the eastern and western platforms in the mid and lower salinity fields. The distribution of the species suggests a tolerance of a considerable range of salinities, *e.g.* in the period 1986-1987, in the northern part of the estuary the species tolerated salinities from 21-62 ‰, while in an area marginal to the deltaic field in the southern estuary it experienced salinities of 21.5-32.5 ‰. At most sites, at some sampling times, there was a general trend of declining abundances during May, which correlated with winter fresh water influx. However, the low level of recruitment makes fluctuations in abundance at the various sites difficult to interpret, as they may not be due to mortality and subsequent replenishment of the population by juvenile recruits. Some apparent fluctuations in population density may be an artifact due to the heterogeneous distribution of the species within a habitat, rather than true fluctuations through time, however, changes in mean abundance and lack of overlap in the standard deviation at many sites, and the synchronous nature of the fluctuations between some sites suggests otherwise. The synchronous fluctuations in population density at sites D21 and D22 over 1985 to 1987 may be due to the fact that the northern basin, with more restricted circulation generates a relatively homogeneous large scale habitat that results in similar widespread response in the species. Unlike many other species in the estuary, *T. deltoidalis* did not exhibit a decline in the abundance during the study.

The histograms indicate that there is periodic juvenile recruitment, and a progressive shift in the mode of shell sizes as the individuals grow and mature. Further, the age structures from the different environments (*e.g.* platforms sites *vs* basins, lower estuarine sites *vs* middle or upper estuarine sites) show slightly to markedly varying structure and history, suggesting there is a range of factors regulating the populations (*viz* the varying relative importance of mortality due to factors of the physical environment, mortality due to disease, predation, and possibly migration between habitats). The appearance of juveniles in August 1982 along Transect C, in August and December 1983 along Transect A and in the central basin, in August 1985 along Transect A, and in September 1986 along Transect A appears to correlate with some peaks in population density for those times (*e.g.*, the August 1982 recruitment coincides with increases in population density at sites A3, A4, B11, C17; the the August and December 1983 recruitment appears to coinicide with a lagged increase in population densities at sites A3, A4 and C17; the December 1985 recruitment appears to coinicide an increase in population density at A4). For the most part, however, the appearance of juveniles did not always correlate with peaks in population abundance, and so it is difficult to interpret some of the abundance variations. Population age structures indicate that the populations were maintained by a continuous but sporadic low level of juvenile recruitment.

Tellina deltoidalis is common from Queensland to Western Australia, including Tasmania (Wells & Bryce 1985). Chalmer *et al.* (1976) listed *T. deltoidalis* as a continuous and common resident of the sand flats of the lower and middle parts of the Swan Estuary, and also noted that it is occasionally collected in the sea near Fremantle. Wells & Threlfall (1981) recorded it on shallow water sand flats in the Peel-Harvey Estuary. Chalmer & Scott (1984) recorded it in Leschenault Inlet during their 1974 survey. The seasonal pattern of decline in abundance of the species is probably not related to seasonal senescence of mature individuals but perhaps to predation, as their shallow subtidal habitats do not exhibit extremes of temperature and salinity. Also, studies in the Peel-Harvey Estuary show a seasonal pattern of microalgal blooms in late winter to early summer, driven by an influx of nutrient-rich fresh water during winter (*e.g.* Lukatelich & McComb 1983; Lukatelich 1986). This pattern of algal response to an influx of nutrients may occur in Leschenault Inlet although at a reduced level, *i.e.* nutrients are imported into the estuary, and generate short term phytoplankton blooms seasonally, or phytoplankton are transported into the estuary from the drainage basin during winter (Hosja & Deeley 2000). If so, nutrient influx, or fluvial delivery of phytoplankton, would result in a seasonality in food supply for suspension and deposit feeders, and may explain the apparent seasonal trends observed for the species. For the northern sites, along Transect D, the conditions during summer of high salinities and temperatures would presumably be an additional limiting factor for the species in this hydrochemical zone.

Nassarius burchardi

Nassarius burchardi was ubiquitous in the Leschenault Inlet estuary, even moving into tidal habitats during high tide, but was uncommon in the upper estuarine salinity field. Population densities of *N. burchardi* fluctuated independently of trends in environmental parameters. Also, there was a decline in the abundance of the species in the estuary since the beginning of the study, particularly noted along Transect A. The population had been composed primarily of mature individuals, and the sporadic, low level juvenile recruitment which occurred but was insufficient to maintain the population at its original levels of abundance. This pattern of population maintenance contrasts with the results of Smith (1975) in the Swan Estuary where populations were maintained by two spawning seasons per year, despite an annual decrease in numbers following seasonal fresh water input. The population structures in Leschenault Inlet suggest that the species is relatively long lived, with stable adults and low levels of recruitment, or that its juvenile phase is a short-lived, rapidly-growing phase (similar to that proposed by Wells & Keesing 1997 for *Haliotis roei*).

N. burchardi is common elsewhere in many south-western Australian estuaries and locally in marine environments (Smith 1975; Chalmer *et al.* 1976; Wallace 1975; Chalmer & Scott 1984). The species was recorded in Leschenault Inlet in 1973 by Smith (1975) and in 1974 by Chalmer & Scott (1984). Kowarsky (1969) and Smith (1975) studied *N. burchardi* in the Swan River Estuary, where it inhabited all substrate types at all depths, though it was eliminated from the shallow sand flats by fresh water during winter where salinities are > 7 ‰. Smith (1975) suggested that deep water populations provided adult and sub-adult immigrants and larvae which repopulate the shallow water flats during spring. *N. burchardi* spawns twice annually, in late autumn and in early spring (Smith 1975). The smallest observable individual in the field was 5 mm in shell length; in the laboratory, animals reached adult size in eleven weeks, with a growth rate of 2 mm month^{-1} (Smith 1975), and growth rates determined from populations in the field were 1.4 mm month^{-1}. Growth rates of *N. burchardi* were affected also by temperatures, with adult size reached in 24 weeks at 15 °C, and in 11 weeks at 20-25 °C. In most *Nassarius* species, when the adult maximum size is reached the outer lip and callus thicken.

In laboratory experiments, Smith (1975) found that the species tolerates a wide range of salinities at all stages of its life cycle. Smith's results were applied to the Swan River Estuary, with the experiments involving only salinities lower than sea water. No eggs hatched below 10.5 ‰, implicating salinity as an environmental regulator of the species, as the success rate of laying/hatching increased with increasing salinity. In adults, 7 ‰ was the minimum salinity for activity, and animals which were acclimatized to 35 ‰ were able to tolerate instantaneous drops to 17 ‰ (withdrawal of the animal into the shell serving as a mechanism for avoidance). Whereas an instantaneous reduction in salinity from 35 ‰ to 13 ‰ results in temporary retraction from which the animal recovers after acclimatization, a drop from 35 ‰ to 10 ‰ results in death (Kowarksy 1969; Smith 1975), implicating fresh water as a potentially lethal factor. In summary, *N. burchardi* populations in the Swan River Estuary had two breeding periods per year, a rapid growth rate (taking 5 months to develop from egg to sexually mature adults), a tolerance of wide salinity ranges by eggs and adults, and a high mobility of individuals enabling migration (Smith 1975). These aspects enabled the species to adapt to the estuarine environment.

The significance of the laboratory and autoecological results, described above, for the Leschenault Inlet situation is that mortality due to salinities of < 7 ‰ may occur at some sites and not at others, migration between sites may occur and juvenile recruitment may be frequent. In the Leschenault Inlet estuary, however, the vast majority of adult *N. burchardi* examined had a thickened outer lip and callus, indicating that they were mature and had ceased growing. Juvenile recruitment was generally low, with individuals < 6 mm in size rarely comprising more than 2% of the population. Juvenile recruitment alone did not account for the local increases in abundances, and given the decrease in population numbers since the beginning of the study, it appears this level of recruitment was insufficient to maintain the population density first encountered in the study. These results suggest a gradually depleting population of mature *N. burchardi* over the period of study.

There are no data for Leschenault Inlet on spawning times and growth rates of juveniles for *N. burchardi*, and so the Swan River Estuary data (Smith 1975) are used to interpret patterns in the Leschenault Inlet estuary. It must be borne in mind, however, that patterns for the species in the Swan River Estuary (with its own set of environmental parameters) could be different to those of the Leschenault Inlet estuary. In the Leschenault Inlet estuary, there had been some generally low levels recruitment of juveniles of *N. burchardi* from 1982 to 1984, *e.g.* along Transect A in February 1984, and significant recruitment along Transects A and B by February 1985. Extrapolating the data of Smith (1975), juveniles of 5-6 mm size would have developed from eggs laid 10-11 weeks earlier, suggesting a spawning the previous mid-December. Juveniles of 5.0-5.9 mm in size taken along Transect A in May 1985 would have developed from eggs laid during the previous mid-March. By December 1985, the populations along Transect A were unimodal with a mode centred around 9 mm, as they had been for most of the study period, implicating rapid juvenile growth. In seven months, the juveniles of May 1985 (< 6 mm) had joined the adult population of 8-9 mm, indicating a growth rate of *ca* 0.6 mm per month. Some juvenile recruitment occurred along Transect A in May 1986 and

September 1986, arising from spawning in mid-March and mid-to late July, respectively. Juveniles were not recorded for the remainder of the study.

The trends in population age structures of *N. burchardi* in Leschenault Inlet estuary indicate firstly that recruitment, albeit at low levels, occurred primarily in the lower estuary, and rarely in mid-estuary (possibly due to the higher salinities there), and secondly, that recruitment of juveniles could occur in any month. No juveniles were recorded at Transect D, where the species is generally absent. Recruitment of juveniles does not appear to correlate with changes in population abundances at various sites (*e.g.* there was a peak in abundance between December 1984 and February 1985 at B9 but no juvenile recruitment).

Spisula trigonella

Spisula trigonella occurred at all water depths and on all substrate types, from the coarse sands of the Collie River delta to the mud of the central basin, but it was extremely abundant in specific habitats such as the central basin muds in the estuary at the beginning of study. The populations, however, were not maintained at their original densities. Toward the end of the study period the species was uncommon, or rare, or absent at the study sites. Given that elsewhere in south-western Australia *Spisula* is considered to be of marine affinity (Chalmer & Scott 1984), individuals comprising the estuarine populations here would have derived as plankton from the (oceanic) Koombana Bay populations.

Chalmer & Scott (1984) recorded the species in the Leschenault Inlet estuary in 1974 but in low abundance. Similarly, during the initial reconnaissance survey of this study, in February 1982, the species was present but not abundant. However, by May 1982, juvenile *S. trigonella* were very abundant in some habitats. Just as abruptly, their numbers fell by late 1983 and the species was again uncommon in the estuary by the end of the study period.

The decline in numbers of *S. trigonella* between December 1983 and February 1984 is difficult to explain. Laboratory studies suggest the species tolerates quite low salinities (Hughes 1973), but low salinity does not fully account for decreases in population densities in Leschenault Inlet, as the decline in numbers at many sites occurred despite fluctuating seasonal salinity. At C17, for instance, the peak of *Spisula* abundance occurred between May and December 1982, a period which includes the winter freshening of the estuary, and began to decline by February 1983. However, there was a decline in population numbers at Sites A2 and A3 that might have been linked to a particularly heavy input of fresh water from the Collie River during the 1983 winter, and a consequent generally low salinity during early July of that year, perhaps beyond the level of the salinity tolerance of the species. There also was low salinity along Transect B during July 1983, which persisted until August 1983, during which time when the populations of *S. trigonella* declined. However this decline in *Spisula* numbers appears as a continuation of a trend from February 1983. Further, one of the sampling sites distant from "The Cut", along Transect C, supported the greatest density of individuals, implicating fresh water as a regulatory factor in areas near the Collie River delta.

Marked and dramatic fluctuations in abundance of *S. trigonella*, as recorded in this study, have been noted elsewhere in Australia by Wilson & Kendrick (1968), Stephenson *et al.* (1977), Stejskal (1985) and Rose (1994). It would appear that this pattern of marked population changes is typical of the species, although the reasons underlying these short term invasions of estuaries are unclear.

Throughout this study, populations of *S. trigonella* were dominated by the same age cohort at all times and were not maintained by further recruitment. This population probably originated from larvae outside the estuary, but once established, the greatest density of individuals occurred in localities towards the north of the inlet, away from the marine source. Since the species is a suspension feeder, its food supply is not related to the occurrence of other molluscs. However, the species itself may be prey for carnivorous molluscs. Although predation may account in part for some of the decline in numbers of *S. trigonella* over the study period, it does not explain the overall decline of the population. Clearly, other factors may be operating (*e.g.* breeding biology, fecundity, disease, and a short life span). Interestingly, as the population throughout the estuary of *Spisula*, which was derived from the *Spisula* recruitment in 1982, grew in size, a bimodal size structure of the total population emerged due to different growth rates of individuals in the estuary: in 18 months, the southern populations attained sizes of 18-22 mm, while the northern populations with slower growth rates attained sizes of 10-14 mm. This slower growth may be due to stunting induced by the generally slightly higher salinities in the mid estuarine salinity field, or by a lack of food resources. In contrast, the bimodality of populations evident in August 1983 was due to an influx of juveniles along Transect A, superimposed on an established adult population. In this context, the bimodality of the estuary-wide populations evident in February 1983 was due to differing growth rates from south to north along the estuaty, while that in August 1983 was due to a genuine juvenile recruitment.

The Mactridae have a world-wide distribution in all waters. *S. trigonella* is found around the entire Australian coast from a range of marine and estuarine habitats including shoals and flats at the mouths of rivers (Wilson & Kendrick 1968; Stephenson *et al.* 1977; Stejskal 1985). Lamarck (1818) first recorded the species in Western Australia at Shark Bay. It was also collected off Troughton Island in the far north in 1962. In Western Australian estuaries, the species has been recorded in the Swan River Estuary since 1965 (Wilson & Kendrick, 1968; Chalmer *et al.* 1976), and in Nornalup Inlet (Hodgkin & Clarke 1988). In the Leschenault Inlet estuary, *S. trigonella* was recorded in relatively low numbers in 1974 (Chalmer & Scott 1984) and in Koombana Bay near Bunbury in 1982 (Anon 1982b).

In the Swan River Estuary, the species was recorded as being most abundant on unvegetated sandy substrates, but was also abundant in muddier substrates of deeper water (Hughes 1973). It showed a gradient in size of individuals from upstream to downstream and from deep to shallow water sites, with smaller individuals in upstream and deeper water sites. This was attributed to differential settlement patterns, arising largely due to salinity gradients in the estuary (Hughes 1973), though the Leschenault data implicates differing growth rates as an explanation. Winter fresh water appears to eliminate much of the population. Laboratory studies suggest that 3-4 ‰ is a "lethal minimum salinity", and that juveniles are more tolerant of lower salinities than adults (Hughes 1973). The relevance of these results from the Swan River Estuary to the populations in Leschenault Inlet is that salinity may not be a major factor in regulating *Spisula* populations.

Hydrococcus brazieri

Hydrococcus brazieri is a very shallow water to tidal species that inhabits sandy or muddy sand sites, with a preference for tidal sand habitats in the mid and upper estuarine salinity fields. There was an overall decrease in the abundance of this species from the beginning of the study. Decreases in abundance also occurred intra-annually at any time of year. At some sites this occurred in late summer to early winter, which would seem to implicate high salinities (at the end of summer) and freshwater (at the beginning of winter) as regulating factors. However, the experimental evidence would suggest otherwise (see later), and overall, in the Leschenault Inlet context, *H. brazieri* appeared to be tolerant of high salinities and temperatures, as the changes in its population densities did not correlate with extremes in these water parameters. Variation in its population numbers, however, may also be due to natural patchiness, or to predation.

H. brazieri occurs around the Australian coastline from New South Wales to Tasmania and to Western Australia, including many Western Australian estuaries (Wells & Threlfall 1981). It was found in shallow-water sand in the Peel-Harvey Estuary, in densities of up to 10 000/m^2 (Wells & Threlfall 1982a,b,c). There, animal densities fluctuated markedly but apparently not in direct response to any seasonal pattern similar to that observed in Leschenault Inlet. It was recorded in Leschenault Inlet in 1974 by Chalmer & Scott (1984).

Laboratory experiments show that the species is tolerant of a wide range of salinities and temperatures, with preferences for certain combinations of temperatures and salinity between 10 ‰ and 50 ‰ (Wells & Threlfall 1982a). During summer in the period of highest water salinity, the species is active at salinities between 25 ‰ and at least 54 ‰. During winter in times of lowest salinity, the species is active at salinities between 15 ‰ and 35 ‰. Also, *H. brazieri* is tolerant of temperatures between 8 °C and 32 °C. These experimental results indicate that winter conditions would not necessarily eliminate *H. brazieri* from estuaries, and that moderate summer conditions are favorable for the species. In the context of Leschenault Inlet, this means that the species is able to tolerate summer temperature conditions and salinities developed on the tidal flats, and also is able to survive the winter freshening in these environments.

Field studies over two years in the Peel-Harvey Estuary showed *H. brazieri* reproducing continuously, with no obvious seasonality (Wells & Threlfall 1982b). Females attach eggs to any suitable hard surface. Embryos emerge from eggs as crawling juveniles, with individuals reaching maturity in 4 months, reaching maximum size in 7-8 months. Some individuals perhaps might survive for a second year. In this context, the patterns of population fluctuations in Leschenault Inlet may be related to this type of ongoing recruitment.

Other species

The main occurrence of *Acteocina* sp in the tidal, upper estuary field indicates it is tolerant of a wide range of salinities and high temperatures. Its abundance fluctuated markedly temporally, but this did not occur in synchrony with trends in environmental factors. *Acteocina* consumes foraminifera (Burn & Thompson 1998), and fluctuations in foraminifera densities, related to variation in micro-environmental factors such as detritus content (*cf* Hottinger 1983) may well determine the densities of this species. Although fluctuating, the overall level of abundance of the species had been maintained during the study period.

The remaining species were either quite widespread (*e.g. Bedeva paivae* and *Sanguinolaria biradiata*), occurred in low numbers in consistent but restricted distributions (*e.g. Assiminea*), or formed temporary localized but quite dense populations or became established as low density populations later in the study period (*e.g. X. securis* colonising the Collie River delta for one year, and a small population of *Bittium granarium* of a mixed-size structure locally colonising the lower estuary). In the context of the numerically more dominant species discussed above, these less common species appeared to have little effect on the overall ecosystem of Leschenault Inlet, regardless of their trophic level.

For *Bedeva paivae*, the data suggest a continuous presence during the study period. Due to its low density, fluctuations in abundance of the species may be an artifact of sample area and sample number, rather than population dynamics. Biogeographically, *B. paivae* is widespread (Wells & Bryce 1985). Chalmer *et al.* (1976) record it in the Swan River Estuary, and Wells & Threlfall (1981) recorded it in the Peel-Harvey Estuary. In this study, in contrast to its occurrence in rocky estuarine settings elsewhere in south-western Australia, *B. paivae* inhabited muddy to sandy subtidal shallow water platforms.

Xenostrobus securis occurs throughout southern Australia (Wilson 1968). It was recorded in the Peel-Harvey Estuary (Wells & Threlfall 1981), and is a sporadic and temporary resident of the Swan River Estuary (Chalmer *et al.* 1976). Studies of the species in the Swan River Estuary was within the context of a freshwater to marine gradient (Wilson 1968) and not under conditions of salinities above that of sea water. Consequently, the results are not applicable to the Leschenault Inlet estuary where salinities rise above that of seawater, but only to the Collie River to estuary transition. Normal development of embryos of *X. securis* occurs between a salinity of 8 ‰ and 17.5 ‰, which would preclude the possibility of marine dispersal of larvae between estuaries (Wilson 1968). If so, then populations resident in the Collie River delta in 1982 would have originated from populations further upstream.

There is little information on *Assiminea* sp. Its distribution in this study indicates a tolerance of a range of salinities and temperatures. Wells (1984) notes *Assiminea* sp as inhabiting salt marshes in several south-western Australian estuaries, although its full geographic range is unknown, and Chalmer *et al.* (1976) note it in the Swan River Estuary.

Classification of estuarine molluscs

There is a wide range of approaches to the classifying of estuarine fauna. Day (1981) presents a classification based on the salinity tolerance of the species and its occurrence, or otherwise, in the marine environment, and divides estuarine fauna into six categories. Of these, four are relevant to the mollusc fauna of the Leschenault Inlet estuary:

- the stenohaline marine component - including species which are represented in the marine environment and which can tolerate salinities of between 25-40 ‰;
- the euryhaline marine component - including species which are represented in the marine environment and which tolerate salinities of 5-50 ‰;
- the true estuarine component - including species which have no representation in the marine environment and which tolerate salinities of 20-60 ‰; and
- the euryhaline fresh water component - including species primarily derived from fresh water but which are able to tolerate salinities greater than 5 ‰.

Based on available marine records to determine occurrence of a given species with the marine to estuarine transition (Chalmer *et al.* 1976; Wells 1984; Wells & Bryce 1985), studies of the salinity tolerances of individual species (Wells & Threlfall 1982a; Wilson 1968; Hughes 1973; Smith 1975), as well as the distribution of species within Leschenault Inlet in relation to the salinity fields documented during this study, the molluscs of the Leschenault Inlet estuary are classified as follows (an * indicating a tentative assignment due to absence of distribution information and limited occurrence in Leschenault Inlet):

- the stenohaline marine fauna: *Bittium granarium;* *Cerithiopsidae sp, **Mactra flindersi, Mytilus edulis, Polinices conicus, Pholas australasiae, Nassarius nigellus, Solemya australis, Irus crenata, Venerupis anomala.*
- the euryhaline marine fauna; *Tellina deltoidalis, Tellina* sp, *Theora lubrica, Sanguinolaria biradiata, Philine angasi, Nassarius burchardi, Bedeva paivae, Spisula trigonella, Epicodakia* sp, *Laternula creccina,* and
- the true estuarine fauna; *Acteocina* sp, *Arthritica semen, Xenostrobus securis, Hydrococcus brazieri, Fluviolanatus subtorta, Assiminea* sp, *Salinator* sp.

This study has shown that species populations vary markedly in the long and short term, largely independently of seasonal trends in habitat features. Further, the general trends in abundance are different for each species. Obviously, data from different times would result in different assemblages being identified (*cf* Cresswell *et al.* 2000). However, using long-term data available in this study, seven molluscan assemblages/populations, determined by the most abundant and/or temporally persistent components, are provisionally noted below as to their occurrence in the various habitats (minor molluscan components of an assemblage or population are not incorporated into the nomenclature):

- a mixed assemblage, of the tidally flushed environments of the Preston River delta and the tidal delta;
- a *Tellina* (± *Spisula*) dominated assemblage inhabiting the deep water central muddy basin;
- a *Tellina-Nassarius* (± *Bedeva*) dominated assemblage inhabiting seagrass-vegetated platforms;
- a *Tellina*-dominated population inhabiting shallow subtidal mud flats.
- a *Hydrococcus*-dominated population inhabiting tidal sandy beaches;
- an *Acteocina*-dominated population inhabiting tidal mud flats;
- an *Arthritica*-dominated population inhabiting low tidal to very shallow subtidal sand and muddy sand flats.

The full picture of associations and population occurrences in time and space is more complex, but generalised distributions of the main mollusc species are shown diagramatically for the various habitats in lower, middle and upper parts of the estuary in Figure 16. The relative abundance of species of each assemblage will vary.

The results of this study suggest a complexity of biological responses among species of the estuarine mollusc fauna. However, despite the medium-term nature of this study, and the fact that a habitat framework types was used within which to interpret patterns in the species abundances, much of the population dynamics of mollusc species still remains unexplained in detail. While various large scale and macroscopic features of the estuary were identified as a habitat framework for benthos, it may be that many species respond to micro-environmental features only indirectly related to the macroscopic setting, *e.g.* microscopic algal distribution related to substrate grain size. A fuller explanation of the autecology of the various species in the Leschenault Inlet estuary must await research on its micro-habitat features, examining the relationship between macroscopic setting and benthos through factors such as water temperature, salinity, oxygen concentration, substrate texture and detritus content, substrate temperature, pore water characteristics, and bathymetry, at smaller temporal and spatial scales.

While the abundance of some species could be related to seasonal changes in salinity, there was a general lack of direct correlation between evident annual salinity patterns and the abundance of many of the commonly occurring species. This suggests that the species are adapted to cope with fluctuations in salinity in the estuary. The patterns of population abundance may be influenced by parameters such as food supply, and predator/prey relationships (*e.g.*, predators such as birds and fish). These aspects of the estuarine ecology require investigation in order to fully understand the mollusc population dynamics. While studies have been already carried out on species such as *Arthritica semen, Hydrococcus brazieri, Nassarius burchardi,* *Spisula trigonella*, and *Xenostrobus securis*, the reproductive biology and the variation of autecology between these and other species in the Leschenault Inlet estuary needs to be understood to explain the population dynamics of molluscs species specifically in this estuary.

In summary, the range of potential factors that control the abundance and composition of the molluscs, and hence composition of assemblages in Leschenault Inlet estuary are manifold, and appear to be complex in their interaction. Firstly, there is the effect of the physical environment. This may affect species distribution through features of the habitat such as substrate, depth, and salinity field (*e.g. Arthritica* in shallow water to tidal sand, *Acteocina* in tidal mud), and hydrochemically by seasonally regulating the populations of some species (*e.g.* freshwater influx annually may eliminate or trigger migration of populations of *Nassarius*, and cause mortality of *Spisula*). The significance of substrate in directly or indirectly determining distribution of benthic molluscs is well established (Parker 1975; Yonge 1976). For instance, the distribution of deposit feeders can be related to particle size as it affects their food source and feeding (Tunnicliffe & Risk 1977). In another example, the control on mollusc distribution and abundance of depth, grainsize, salinity and temperature was investigated by Wells (1978) who found that of eight environmental variables investigated, depth and grain size were the most important in controlling the density of the mud snail *Hydrobia* on a Nova Scotia salt marsh.

Other factors regulating composition of mollusc assemblages include the effects of predators, local population explosions, style of recruitment, the various mechanisms of population maintenance, and the interactions of long term population patterns between the species. In regard to the effects of local population explosions, clearly, rapid increases in population numbers can have a marked effect on assemblage composition as exemplified by *Spisula* which exhibited a major increase in numbers, and then subsided. Similar patterns of population explosions exhibited by other species in this estuary are afforded by an ophiuroid species (*cf* Unno 2000) and polychaetes (*e.g. Capitella capitata; cf* TA Semeniuk 2000), and in concert, can result in varying and complex faunal associations through time. The varying types of population dynamics and maintenance is exemplified by the contrasting patterns shown by *Tellina*, *Spisula*, and *Nassarius*. The varying styles of recruitment *i.e.* juvenile recruitment *vs* adult or post-juvenile migration, and the effects of recruitment from intra-estuarine larvae *vs* marine-derived larvae and how they influence population maintenance, is afforded by examples of *Tellina* which exhibited recruitment throughout the study, and *Nassarius* which did not appear to exhibit recruitment but rather inter-site migration. Finally, composition of assemblages can be markedly affected where there were long term trends of population decline superimposed on the annual input/output of the species, operating synchronously with another species that maintains its populations albeit with seasonal fluctuations. This all creates, within the appropriate salinity and habitat fields, population size and compositional complexities even at the one site, and differences in response and complexity between sites.

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Appendix 1. Mean abundance of key species of mollusc per square metre (abundances > 10/m² are rounded off) at the various sites (see Fig 1).

Acteocina sp

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	170	0	0	0
Aug-82	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	51	0	0	*
Dec-82	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	74	128	9.6	3.2
Feb-83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.6	0	0	0	0	9.6	3.2	13
May-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	3.2	3.2	*
Aug-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	9.6	0	*
Dec-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	9.6	*	0	*	0	86	6.4	*
Feb-84	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	58	0	0	0	38	19	13	90
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	45	26	9.6	9.6
Aug-84	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	22	26	3.2	16
Dec-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	19	*	0	*	0	16	83	6.4
Feb-85	0	0	0	0	0	0	0	29	0	0	0	0	0	0	16	0	0	0	32	0	32	22
May-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	6.4
Aug-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	115	0	0
Dec-85	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	22	26	3.2	16
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	9.6	0	16	*
Aug-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	54	46	0
Sep-86	0	0	0	0	0	0	9.6	3.2	0	0	0	0	0	0	3.2	0	0	0	6.4	16	76	22
Oct-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	13	13	54
Nov-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	19	35	83
Dec-86	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	16	106	70
Jan-87	0	0	0	0	0	0	0	*	0	*	0	*	*	*	0	*	0	*	0	29	80	54
Feb-87	0	0	0	0	0	0	0	*	0	*	0	*	*	*	0	*	0	*	0	106	67	112
Mar-87	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	29	64	61

Arthritica semen

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
May-82	815	0	0	127	688	0	3440	2319	1529	561	510	0	255	306	662	25	1885	1350	25	51	1885	255
Aug-82	*	1376	0	127	*	*	*	*	331	*	0	*	*	*	764	*	1885	484	*	1350	3593	*
Dec-82	*	815	0	102	*	*	*	*	669	*	0	*	*	*	943	*	3236	102	*	2892	4026	*
Feb-83	12689	3159	0	76	2777	382	510	459	688	51	0	0	306	1529	917	102	4637	229	*	3159	16052	127
May-83	*	892	0	178	*	*	*	*	408	*	51	*	*	*	1248	*	1885	178	*	382	*	*
Aug-83	*	3949	0	153	*	*	*	*	790	*	0	*	*	*	178	*	713	51	*	1401	3516	*
Dec-83	*	1019	0	1096	*	*	*	*	1045	*	76	*	*	*	1987	*	2344	0	*	3026	10854	*
Feb-84	0	178	0	382	25	25	178	688	382	586	102	0	0	76	2675	1198	357	0	408	1987	7924	1223
May-84	*	0	0	0	*	*	*	*	535	*	0	*	*	*	0	*	0	0	*	229	994	1554
Aug-84	*	0	0	102	*	*	*	*	0	*	0	*	*	*	280	*	0	357	*	178	357	1427
Dec-84	*	0	0	0	*	*	*	*	25	*	51	*	*	*	357	*	331	0	*	3007	1631	1809
Feb-85	459	51	0	102	0	0	101	204	178	0	306	0	178	357	0	0	0	229	0	0	153	0
May-85	*	1147	408	280	*	*	*	*	0	*	153	*	*	*	153	*	153	0	*	1172	815	917
Aug-85	*	102	127	76	*	*	*	*	25	*	0	*	*	*	0	*	0	0	*	255	76	0
Dec-85	*	306	229	178	*	*	*	*	0	*	0	*	*	*	25	*	25	51	*	0	0	0
Feb-86	178	51	204	51	0	178	255	204	76	0	0	0	76	153	229	0	255	178	0	0	127	0
May-86	153	204	153	25	0	178	127	178	96	25	25	0	51	51	76	0	280	76	0	0	127	0
Jun-86	0	0	76	51	0	178	510	102	127	153	0	*	0	0	357	0	382	51	127	0	0	0
Jul-86	*	0	0	0	*	*	*	*	0	*	764	*	*	*	204	*	0	0	*	0	2344	*
Aug-86	*	739	0	459	*	*	*	*	382	*	0	*	*	*	0	*	255	0	*	0	0	0
Sep-86	459	433	0	0	0	0	0	1045	535	815	0	25	204	255	331	255	662	0	280	0	51	357
Oct-86	*	4255	178	357	*	*	*	*	459	*	0	*	*	*	280	*	484	0	*	0	0	0
Nov-86	*	51	178	0	*	*	*	*	0	*	204	*	*	*	0	*	1682	662	*	0	229	0
Dec-86	7364	0	586	255	3414	0	0	2089	1096	3083	815	586	586	2548	306	1198	3796	280	1274	2956	8791	1198
Jan-87	*	5657	1987	1350	*	*	*	*	764	*	1198	*	*	*	917	*	2548	1045	*	2370	10217	484
Feb-87	*	76	357	0	*	*	*	*	1427	*	0	*	*	*	0	*	4383	1274	*	11415	13606	0
Mar-87	0	866	331	0	0	178	14422	1198	0	0	459	1121	0	0	0	1529	3618	0	357	1784	5657	484

Appendix 1 (continued).

Bedeva paivae

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	1.6	*	*	0	*	1.6	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	3.2	3.2	0	0	6.4	0	3.2	0	0	0
Aug-82	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Dec-82	*	3.2	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	6.4	*	0	0	0	0
Feb-83	0	0	9.6	0	0	0	3.2	0	6.4	16	0	0	9.6	0	3.2	0	3.2	0	0	0	0	0
May-83	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	13	*	0	0	0	*
Aug-83	*	13	0	0	*	*	*	*	3.2	*	3.2	*	*	*	9.6	*	0	*	0	0	0	*
Dec-83	*	0	0	3.2	*	*	*	*	0	*	0	*	*	*	0	*	6.4	*	0	0	0	*
Feb-84	0	0	35	0	0	0	0	0	0	3.2	0	0	0	3.2	3.2	3.2	0	0	0	0	0	0
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	3.2	*	3.2	0	0	0
Aug-84	*	0	0	0	*	*	*	*	6.4	*	0	*	*	*	3.2	*	0	*	3.2	0	0	0
Dec-84	*	0	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	3.2	*	0	0	0	0
Feb-85	0	0	3 2	0	0	0	3.2	0	32	19	0	3.2	0	6.4	0	0	0	0	6.4	0	0	0
May-85	*	6.4	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-85	*	0	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	3.2	*	3.2	0	0	0
Dec-85	*	0	0	0	*	*	*	*	6.4	*	0	*	*	*	3.2	*	0	*	0	0	0	0
Feb-86	0	0	0	0	0	0	0	0	3.2	3.2	0	0	0	0	0	6.4	0	0	0	0	0	0
May-86	0	0	0	0	0	0	3.2	0	9 6	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	9.6	9.6	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	6.4	3.2	0	*	*	*	*	13	*	0	*	*	*	3.2	*	0	*	0	0	0	*
Aug-86	*	0	0	0	*	*	*	*	6 4	*	0	*	*	*	0	*	0	*	0	0	0	0
Sep-86	0	0	0	0	0	0	0	3.2	3.2	0	0	0	0	16	3.2	6.4	0	0	0	0	0	0
Oct-86	*	0	3.2	3.2	*	*	*	*	22	*	0	*	*	*	3.2	*	9.6	*	0	0	0	0
Nov-86	*	3.2	0	0	*	*	*	*	26	*	0	*	*	*	6.4	*	0	*	0	0	0	0
Dec-86	0	0	0	0	0	0	0	3.2	9.6	0	0	0	3.2	0	0	3.2	0	0	0	0	0	0
Jan-87	*	0	3.2	0	*	*	*	0	6.4	0	3.2	0	*	*	0	*	3.2	*	0	0	0	0
Feb-87	*	3.2	0	0	*	*	*	*	16	*	0	*	*	*	6.4	*	0	*	0	0	0	0
Mar-87	0	3.2	16	0	0	0	0	0	9.6	0	0	0	3 2	3.2	0	0	0	3.2	0	0	0	0

Hydrococcus brazieri

A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22	
Feb-82	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3974	0	0	0
Aug-82	*	0	0	0	*	*	*	*	*	*	3.2	*	*	*	0	*	0	*	16944	0	0	*
Dec-82	*	0	0	0	*	*	*	*	*	*	0	*	*	*	45	*	0	*	16176	134	0	0
Feb-83	0	0	0	0	22	0	3 2	0	0	0	0	0	0	0	6.4	0	0	0	15008	9.6	3.2	0
May-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	3 2	*
Aug-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	9.6	0	*
Dec-83	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	0	32	0	*
Feb-84	0	0	0	3.2	0	0	0	3.2	3.2	0	0	0	0	3 2	0	0	0	0	0	3.2	9.6	6 4
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	99	*	0	*	32	0	3.2	0
Aug-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	416	0	0	0
Dec-84	*	0	0	0	*	*	*	*	22	*	0	*	*	*	0	*	16	*	0	29	19	0
Feb-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.4	0	0	0	0	0	0
May-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	32	*	0	*	9.6	0	38	6 4
Aug-85	*	0	0	0	*	*	*	*	51	*	0	*	*	*	0	*	0	*	118	0	0	0
Dec-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	416	0	0	0
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.2	9.6	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.6	6.4	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	54	0	0	0
Jul-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Aug-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	131	3.2	6.4	3.2
Sep-86	0	0	0	0	0	0	38	0	0	0	0	0	0	0	19	0	0	0	547	16	0	3.2
Oct-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	1386	42	19	6.4
Nov-86	*	0	0	9.6	*	*	*	*	0	*	0	*	*	*	0	*	0	*	205	61	42	13
Dec-86	0	0	0	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	317	19	3.2	6.4
Jan-87	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	3.2	*	131	19	9.6	0
Feb-87	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	109	35	3.2	3.2
Mar-87	0	0	0	0	0	0	224	13	3.2	0	0	0	0	0	0	0	0	0	570	6.4	13	0

Appendix 1 (continued).

Nassarius burchardi

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	48	93	*	*	6.4	*	674	*	*	*	*	*	*	*	*
May-82	6.4	154	32	486	461	0	61	80	77	106	29	42	378	179	32	128	6.4	3.2	0	0	0	0
Aug-82	*	195	83	931	*	*	*	*	304	*	102	*	*	*	32	*	112	*	6.4	0	0	*
Dec-82	*	202	407	944	*	*	*	*	323	*	166	*	*	*	26	*	131	*	0	0	0	0
Feb-83	6.4	285	250	1446	1907	0	755	170	387	611	211	198	944	128	32	186	154	3.2	0	0	0	0
May-83	*	474	256	1338	*	*	*	*	374	*	93	93	*	*	19	*	51	*	0	0	0	*
Aug-83	*	141	90	845	*	*	*	*	688	*	99	*	*	*	122	*	189	*	0	0	0	*
Dec-83	*	3.2	131	2051	*	*	*	*	627	*	29	*	*	*	45	*	102	*	0	0	0	*
Feb-84	0	3.2	74	938	624	0	230	154	381	410	32	38	749	214	45	122	115	26	0	0	0	0
May-84	*	9.6	16	301	*	*	*	*	35	*	64	*	*	*	0	*	26	*	0	0	0	0
Aug-84	*	3.2	3.2	733	*	*	*	*	182	*	13	*	*	*	32	*	22	*	6.4	0	0	0
Dec-84	*	0	26	58	*	*	*	*	381	*	0	*	*	*	64	*	29	*	0	0	0	0
Feb-85	0	32	22	3.2	470	0	64	48	387	339	61	22	32	106	3.2	51	80	19	0	0	0	0
May-85	*	22	19	13	*	*	*	*	42	*	42	*	*	*	0	*	70	*	9.6	0	0	0
Aug-85	*	0	3.2	83	*	*	*	*	128	*	0	*	*	*	13	*	237	*	0	0	0	0
Dec-85	*	3.2	3.2	733	*	*	*	*	182	*	13	*	*	*	32	*	22	*	6.4	0	0	0
Feb-86	0	9.6	0	42	77	45	150	9.6	48	48	6.4	*	19	16	0	32	9.6	3 2	3.2	0	0	3.2
May-86	26	74	0	6.4	0	0	29	38	202	86	9.6	*	45	9.6	9.6	9.6	9.6	0	9.6	0	0	6.4
Jun-86	3.2	0	0	74	122	0	19	86	70	58	0	*	0	0	3.2	6.4	13	0	0	0	0	0
Jul-86	*	51	42	51	*	*	*	*	285	*	16	*	*	*	29	*	6.4	*	3.2	0	0	*
Aug-86	*	9.6	29	285	*	*	*	*	291	*	26	*	*	*	3.2	*	9.6	*	3.2	0	0	0
Sep-86	0	0	26	42	128	0	19	70	80	42	32	9.6	51	154	9.6	38	13	3.2	0	0	0	3.2
Oct-86	*	0	51	186	*	*	*	*	528	*	16	*	*	*	32	*	19	*	0	0	0	0
Nov-86	*	6.4	3.2	72	*	*	*	*	445	*	22	*	*	*	38	*	6.4	0	0	0	0	0
Dec-86	0	45	86	26	122	0	0	192	211	118	3.2	48	74	35	45	42	26	13	0	0	0	0
Jan-87	*	35	45	29	*	*	*	*	154	*	51	*	*	*	80	*	96	*	6.4	0	0	0
Feb-87	*	6.4	26	42	*	*	*	*	154	*	38	*	*	*	38	*	74	*	3.2	0	0	0
Mar-87	0	45	186	102	115	0	0	141	400	106	13	48	48	48	26	93	6.4	3.2	0	0	0	0

Spisula trigonella

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	3.2	1.6	*	*	3.2	*	*	*	*	*	*	*	*	*	*
May-82	83	570	512	0	0	0	179	16	0	0	6682	11958	0	1.6	0	6.4	13504	0	45	0	0	0
Aug-82	*	1402	384	13	*	*	*	*	0	*	1446	*	*	*	0	*	14186	*	93	0	3.2	
Dec-82	*	1120	4499	0	*	*	*	*	0	*	6925	*	*	*	6.4	*	10902	*	54	0	3.2	0
Feb-83	3.2	1222	2326	0	3.2	0	157	0	0	0	5570	4384	0	0	0	0	2880	0	42	0	0	0
May-83	*	1107	2774	3.2	*	*	*	*	0	*	3456	3296	*	*	0	*	1760	*	35	0	0	*
Aug-83	*	874	723	0	*	*	*	*	0	*	2691	*	*	*	0	*	504	*	32	0	0	*
Dec-83	*	13	1418	0	*	*	*	*	0	*	1434	*	*	*	0	*	125	*	29	0	0	*
Feb-84	0	0	1078	0	0	0	22	0	0	0	38	3.2	3.2	0	0	0	0	0	0	0	0	0
May-84	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-84	*	16	0	0	*	*	*	*	3.2	*	3.2	*	*	*	0	*	0	*	3.2	0	0	0
Dec-84	*	0	9.6	16	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	0	0	0
Feb-85	3.2	0	3.2	3.2	0	0	13	0	0	0	3.2	3 2	0	0	0	0	0	0	0	0	0	0
May-85	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	3.2
Aug-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	13	19	0
Dec-85	*	0	0	0	*	*	*	*	3.2	*	3.2	*	*	*	0	*	0	*	3.2	0	0	0
Feb-86	0	0	0	0	0	3.2	9 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	6.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	6.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	26	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Aug-86	*	3.2	9.6	3.2	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	0	0	0
Sep-86	6.4	30	6.4	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oct-86	*	13	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	3.2	0	0
Nov-86	*	29	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Dec-86	0	3.2	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0
Jan-87	*	3.2	0	0	*	*	*	)	0	0	0	0	0	0	0	*	0	*	0	0	0	0
Feb-87	*	3.2	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Mar-87	0	0	0	0	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0

Appendix 1 (continued).

Tellina deltoidalis

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	8	59	*	*	94	*	130	*	*	*	*	*	*	*	*
May-82	0	0	29	83	109	0	3.2	13	80	147	48	154	90	192	61	54	58	74	3.2	0	35	0
Aug-82	*	0	29	138	*	*	*	*	83	*	170	*	*	*	42	*	83	*	0	0	6.4	*
Dec-82	*	0	6.4	285	*	*	*	*	125	*	99	*	*	*	102	*	51	*	0	0	13	26
Feb-83	0	0	22	166	509	0	80	45	198	108	77	102	7.4	362	70	80	86	77	0	6.4	13	6.4
May-83	*	3.2	6.4	154	0	*	*	*	123	*	48	*	*	*	38	*	80	0	3.2	3.2	6.4	*
Aug-83	*	0	32	243	0	*	*	*	147	*	67	*	*	*	80	*	91	0	0	0	6.4	*
Dec-83	*	0	163	371	0	*	*	*	154	*	109	*	*	*	109	*	70	0	0	38	0	*
Feb-84	0	0	6.4	266	400	0	19	16	96	6.4	80	83	54	61	83	102	90	96	0	26	3.2	0
May-84	*	0	0	102	*	*	*	*	6.4	*	77	*	*	*	32	*	96	*	0	64	6.4	9.6
Aug-84	*	0	0	378	*	*	*	*	29	*	96	*	*	*	16	*	74	*	3.2	38	9.6	9 6
Dec-84	*	0	26	90	*	*	*	*	80	*	115	*	*	*	118	*	77	*	0	19	6.4	9.6
Feb-85	0	0	67	106	256	0	32	9.6	70	16	138	67	26	35	13	45	118	42	6.4	0	18	22
May-85	*	0	0	32	*	*	*	*	6.4	*	0	*	*	*	0	*	6 4	*	0	26	0	0
Aug-85	*	0	0	106	*	*	*	*	0	*	45	*	*	*	0	*	45	*	0	4.4	18	6.4
Dec-85	*	0	0	362	*	*	*	*	29	*	96	*	*	*	35	*	74	*	3.2	53	13	9.6
Feb-86	0	0	0	32	102	0	9.6	32	38	38	16	67	32	26	0	9.6	0	38	3.2	9.6	42	67
May-86	0	0	0	29	6.4	0	0	9.6	19	3.2	3.2	61	90	26	13	19	0	42	0	26	45	61
Jun-86	0	0	0	0	35	0	0	3.2	9.6	70	6.4	*	9.6	16	0	3.2	19	29	0	0	9.6	16
Jul-86	*	0	6.4	214	*	*	*	*	192	*	42	*	*	*	48	*	96	*	0	3.2	6.4	*
Aug-86	*	0	13	170	*	*	*	*	182	*	32	*	*	*	42	*	45	*	3.2	0	0	3.2
Sep-86	0	0	26	240	173	0	6.4	0	70	0	35	26	96	93	38	102	42	32	0	22	3.2	9.6
Oct-86	*	0	3.2	320	*	*	*	*	112	*	29	*	*	*	86	*	64	*	0	13	3.2	0
Nov-86	*	0	13	384	*	*	*	*	170	*	26	*	*	*	77	*	112	*	0	6.4	3.2	13
Dec-86	3.2	0	9.6	86	147	0	0	29	211	29	22	61	61	90	96	67	118	42	0	9 6	6.4	9.6
Jan-87	*	0	0	48	*	*	*	*	154	*	51	*	*	*	80	*	96	*	6.4	35	6.4	6.4
Feb-87	*	0	3.2	83	*	*	*	*	154	*	38	*	*	*	38	*	74	*	3.2	16	0	3.2
Mar-87	0	0	6.4	80	131	0	0	3.2	125	19	45	58	102	102	106	160	29	32	6.4	13	3.2	0

Xenostrobus securis, Assiminea sp *and Sanguinolaria*

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.4	0	0
Aug-82	*	**13**	0	0	*	*	*	*	*3.2*	*	0	*	*	*	0	*	0	*	0	0	0	*
Dec-82	*	**58**	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	0	0	0	0
Feb-83	**141**	**58**	0	0	0	0	0	0	0	*6 4*	0	0	0	0	0	0	0	0	*3.2*	0	0	0
May-83	*	6.4	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Aug-83	*	3.2	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Dec-83	*	0	0	**3.2**,*3.2*	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	0	0	0	*
Feb-84	0	0	0	0	0	0	45	0	0	*3.2*	0	0	0	0	0	0	0	0	0	0	0	0
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Dec-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	0	9.6	3.2	0
Feb-85	0	0	0	0	0	0	0	0	*3.2*	0	0	0	0	0	0	0	0	0	0	0	0	0
May-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	0	0	0	0
Dec-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	0	0	0	*	*	*	*	*3.2*	*	0	*	*	*	0	*	0	*	0	0	0	*
Aug-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Sep-86	0	*3.2*	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0
Oct-86	*	0	*3.2*	*3.2*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	3.2
Nov-86	*	0	0	0	*	*	*	*	*3.2*	*	0	*	*	*	0	*	0	*	0	3.2	0	0
Dec-86	0	0	0	0	**3.2**	0	0	0	0	0	0	0	0	0	*3.2*	*6.4*	0	0	0	6.4	3.2	0
Jan-87	*	*9 6*	3.2	0	*	*	*	0	0	0	0	0	0	0	*3.2*	*	0	*	0	13	6.4	3.2
Feb-87	*	0	0	0	*	*	*	*	*3.2*	*	0	*	*	*	0	*	0	*	0	0	0	0
Mar-87	0	0	0	0	0	0	0	3.2	0	9.6	0	0	0	0	*3.2*	*3.2*	0	0	0	0	9.6	0

* *Xenostrobus* in bold, *Assiminea* in normal font, *Sanguinolaria* in italics.

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Mollusc abundance and associations in Leschenault Inlet estuary

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Abstract

Five years of abundance data for the molluscs of the Leschenault Inlet estuary at 22 sites were analysed to provide preliminary results on patterns of their temporal and spatial variably and their potential associations. Only a limited number of the most commonly occurring species were selected for analysis, and only those collected in February and May for each year 1983-1986 were analysed to provide a consistency of sampling times and places, and to compare results in the same season. The spatial and temporal variation of the mollusc species showed species responded to a south-to-north, along-estuary salinity gradient, and to time. The species were assigned to two groups on the basis of their responses to the intra-estuarine gradient. The first group, *Arthritica*, *Acteocina*, *Hydrococcus* and *Tellina*, generally increased in abundance to the north, though the increases varied markedly between the four species, with *Arthritica* showing least variation between sites, *Tellina* showing a large between-site effect, and *Acteocina* and *Hydrococcus* showing marked effects of site differences. *Arthritica* and *Tellina* decreased in abundance over time whereas the other two species showed little change over time. The second group, *Bedeva*, *Nassarius* and *Spisula*, had a negative response to the south to north gradient *i.e.* abundance decreased markedly, especially for *Nassarius* and *Spisula* as the salinity increased. *Nassarius* and *Spisula* also markedly decreased in abundance over time. There is only a slight decrease in abundance over time for *Bedeva*. Cluster analyses showed year to year changes in mollusc associations, signalling caution in the use of such mathematical approaches to categorize biotic assemblages within complex environments such as estuaries with marked hydrochemical and biotic dynamism.

Keywords: Leschenault Inlet, south-western Australia, estuary, molluscs,
mollusc abundance, mollusc associations, cluster analyses.

Introduction

The molluscs of the Leschenault Inlet estuary are variable in their patterns of distribution and abundance through time and space, with the different species generally exhibiting independent patterns of population dynamics both within a given year, and over a number of years (Semeniuk & Wurm 2000). This variability occurs against a back-drop of a seasonally dynamic hydrology, and within a framework of generally medium-term stable estuarine habitats. The spatial and temporal variability and independence between species renders it difficult to consider the fauna in terms of formal "communities" and to rigorously analyse population dynamics.

The sampling in the Leschenault Inlet estuary undertaken by T A Semeniuk, P A S Wurm and V Semeniuk during 1982-1987 (Wurm & Semeniuk 2000; Semeniuk & Wurm 2000; T A Semeniuk 2000; Deurr & Semeniuk 2000) resulted in a large data set on the biota and their environmental setting, involving 22 field sites, 32 sampling times (temporarily stratified), and eight environmental parameters. Specifically for the molluscs, there were 32 species of mollusc, and for three species there were size/frequency data at each sampling time for each sampling site. The full set of data are currently being systematically analysed, and this will be the subject of a later more comprehensive paper on mathematical techniques appropriate to the analysis of the data, and the resulting trends. However, to provide an indication of patterns of mollusc population dynamics and associations, beyond that provided in Semeniuk & Wurm (2000), a series of preliminary analyses of the data are presented in this paper.

The objectives of this paper are twofold: 1) determine any 5-year trends in population patterns for selected species against the salinity and habitat framework of the estuary; and 2) determine the possible associations of molluscs in the Leschenault Inlet estuary. In this context, this paper supplements the information on molluscs presented at a descriptive level by Semeniuk & Wurm (2000).

Setting

Study Area

Leschenault Inlet is an elongate shallow water estuary in south-western Australia. It has distinctive patterns of hydrodynamics and hydrochemistry, bathymetry and sediment types, features that are useful to differentiate habitats for benthos. Its waters are poikilosaline, with an interplay between daily tide-derived marine water through "The Cut", winter freshwater influx from rivers, run-off, drains and seepage, and summer evaporation. The water body is divided into 4 salinity fields based on mean salinity and its annual variation (Fig 1; after Wurm & Semeniuk 2000):

1. a deltaic field, with salinity varying from hyposaline to mesosaline; mean salinity is slightly less than sea water, with a large variability about the mean;

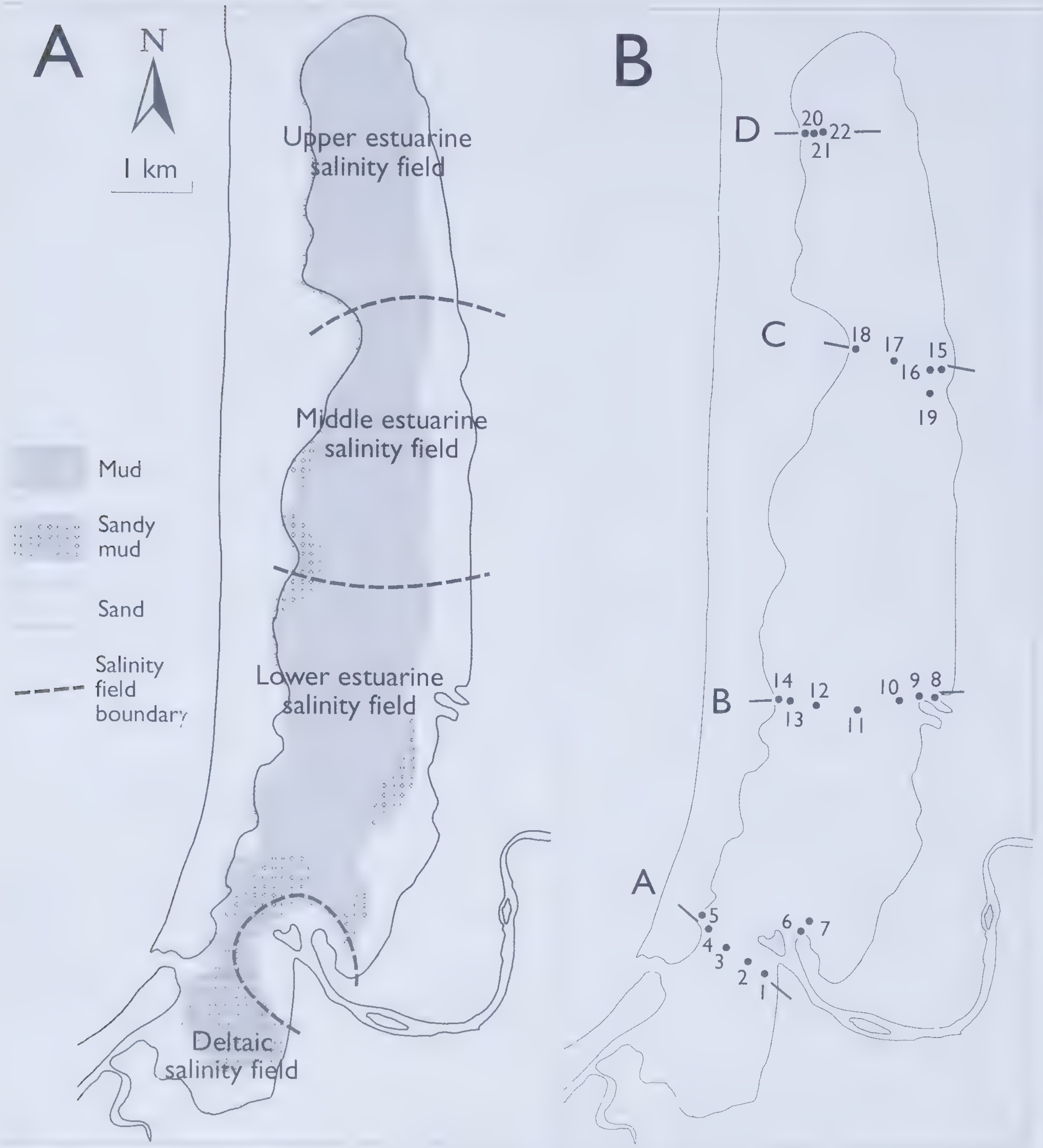

Figure 1. Maps of Leschenault Inlet showing; **A:** the nature of the estuarine salinity fields oriented south-north within the system; and **B:** the location of the sample sites (after Wurm & Semeniuk 2000)

2. a lower estuarine field, with salinity mainly mesosaline; mean salinity is slightly greater than sea water, with a small variability about the mean;
3. a mid estuarine field, with salinity fluctuating within the mesosaline range; mean salinity is higher than sea water, with a large variability about the mean; and
4. an upper estuarine field, with salinity varying annually from hyposaline to hypersalinity; mean salinity is much greater than sea water, with a very large variability about the mean.

In terms of bathymetric setting and substrates, the estuary is divided into several units (Wurm & Semeniuk 2000), four of which are relevant to the background of this paper (Fig 1): 1) a relatively deep water central basin, underlain by mud; 2) a northern shallow water subtidal to tidal flat, underlain by mud; 3) a tidal to shallow water western platform/ramp underlain by muddy sand; and 4) an eastern tidal to shallow water platform underlain mainly by sand.

On the basis of estuarine salinity, bathymetry, and substrates, the estuary can be divided into small-scale habitats (Wurm & Semeniuk 2000). These habitat units provide a framework within which the molluscan fauna were sampled.

The molluscan fauna and their habitats

Thirty two species of mollusc have been recorded in Leschenault Inlet (Semeniuk & Wurm 2000). Six species were common: *Arthritica semen, Tellina deltoidalis, Nassarius burchardi, Spisula trigonella, Hydrococcus brazieri,* and *Acteocina* sp. An additional seven species were present more or less throughout the estuary: *Assiminea* sp *Bedeva paivae, Bittium granarium, Irus crenata, Sanguinolaria biradiata, Solemya australis,* and *Xenostrobus securis,* though not abundant at all times or abundant only sporadically. Generally the molluscs inhabited tidal sand or tidal mud, shallow water platform sand or muddy sand, or deep water basin mud, within lower, middle or upper estuarine salinity fields.

Although present relatively consistently throughout the estuary, and in sufficient numbers to enable description and comparison over five years of study, the six main mollusc species were not always abundant (Semeniuk & Wurm 2000). At times, there were major temporal increases and fluctuations in density of populations, from hundreds or thousands of individuals in a square metre, to zero or less than ten individuals, often with patchiness in abundance resulting in large variance around the mean density for a given site. These fluctuations for the various species were not synchronous. Also, there were times when the density for given species did not markedly vary in time.

Methods

Field methods

The 22 sampling sites of Wurm & Semeniuk (2000) were used in this study. These are numbered 1-22, arrayed along four transects, A, B, C and D that correspond to locations within the four estuarine salinity fields *i.e.* Transect A is in the deltaic salinity field, Transect B is in the lower estuarine salinity field, Transect C is in the middle estuarine salinity field, and Transect D is in the upper estuarine salinity field (Fig 1). Individual sampling sites thus carry notation of transect location and sample site number *e.g.* Site B11 is sample site 11 located along Transect B.

Semeniuk & Wurm (2000) describe two methods for sampling molluscs. All species except *Arthritica semen* were sampled with a square box-corer of size 25 cm x 25 cm x 25 cm. *A. semen*, because of its small size and high abundance, was sampled with a metal cylindrical corer of 10 cm diameter and 15 cm length (to make its abundances comparable to the other molluscs for analysis, the numbers of *Arthritica* in the small corer were multiplied by 7.9). From each site within a habitat, five replicate samples were collected within an homogeneous area of 5 m radius. Because of the large number of sampling sites, involving field surveys and laboratory sorting time, the 22 field sites were variably and selectively sampled during 1982-1986 as follows: sites A2, A3, A4, B9, B11, B11, C15, C19, C17, D20, D21 and D22 were sampled quarterly, and A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18 were sampled annually (Wurm & Semeniuk 2000).

Analytical methods

The full data set in this study encompasses 22 field sites, 32 sampling periods, 32 species, and eight environment parameters (habitat setting, water depth, % mud content in the substrate, salinity, temperature, oxygen concentration, presence of seagrass/algae), resulting in a complex system to analyse. It was decided to trim the data base, selecting the most important attributes, to highlight the results of any numerical classification procedure. Data were analysed using two principal methods, *viz* analyses of abundance trends spatially and temporally after various transformations, and agglomerative hierarchical cluster analyses using Fexible UPGMA to determine relationship of molluscs to environmental setting and possible assemblage associations. Data on mollusc numbers are presented in Appendix 1. A fuller data set is presented in Wurm (1987) and Semeniuk & Wurm (2000).

For the analyses of abundance trends both spatially and temporally, the data used were records for 13 species at 22 sites over 11 sampling times. The values recorded are mean occurrences of each species. The data analysis was carried out in a number of stages. The initial inspection of the data reduced the 13 species to the 7 most abundant species: 1) *Acteocina* sp; 2) *Arthritica semen*; 3) *Bedeva paivae*; 4) *Hydrococcus brazieri*; 5) *Nassarius burchardi*; 6. *Spisula trigonella*; and 7. *Tellina deltoidalis*. Of the 22 sites, only 12 sites (A2, A3, A4; B9, B11, B12; C15, C17, C19; and D20, D21, and D22) were analysed for the 11 sampling times as they were the only sites with complete information for all species and times. The sampling times used were: February 1982, May 1982, February 1983, May 1983, February 1984, May 1984, February 1985, May 1985, February 1986, May 1986, February 1987. For further analyses the sites were grouped into four classes (A, B, C, and D) which are indicative of their locations within the estuary, and hence the salinity levels.

The subsequent analyses first considered all three factors: species (7), sampling times (11), and sites (12), and the three possible two-way interactions, then reduced the sites (4 classes) and the times to linear components. The means for each species classified by the three factors was analysed using a linear model with S-PLUS (Venables & Rippley 1994). Since the data were mean values, the error distribution used was Gaussian, and analysis of residuals was used to confirm the distributional assumptions. If the primary individual counts of occurrences were used, the data could have been analysed as a generalised linear model (GLM) with a Poisson error distribution (McCullagh & Nelder, 1983), but this will be the subject of a later more comprehensive paper.

The analysis of standardised residuals shows significant departures from normality, and a plot of the residuals *vs* fitted values suggested that the variation increases with the mean value, indicating that a logarithmic transformation of the data may be appropriate. The analysis of the raw data was not considered further. Full analysis was of logarithmic transformed data in the form y = log (mean + 0.05). The addition of a small value (0.05) to the raw means was made to overcome the problem of taking the log of zero values. Further analyses using reduced levels of the factors, such as grouping the sites and identifying linear components of time and site (a surrogate for the salinity gradient), were undertaken to highlight the trends in time and/or salinity and their effects on the mean occurrences of the species. Analysis of site groups, where the 12 sites are regrouped into four classes (A, B, C, and D), was used to reflect the salinity gradient within the estuary. Analysis of a linear trend in the four site classes, where the 4 site classes (A - > 1, B- > 2, C - > 3, and D - > 4) were used to indicate that there is a gradient dependent on site class *i.e.* a salinity trend up (down) the estuary. The process of linear trend analysis was further simplified by reducing the 10 degrees of freedom for time to a linear trend over time. The times were "ordered" so that positive (or negative) linear trends for time would indicate increases (or decreases) in overall species occurrences over time. Interactions, especially of species with time, would indicate that species occurrences are not consistent across time(s) for all species *i.e.* some species may decrease over time while others remain stable or even increase. The final linear model included main effects of species, time trend, and site class trend, with interactions of species with time trend and species with site class trend. No other effects have been included.

Only data from the February surveys between 1983 and 1986 were analysed using agglomerative hierarchical clustering (Flexible UPGMA of PATN) in which equal weight is given to objects not groups (Everitt 1974; Belbin 1995) used in this analysis, since during these surveys all 22 sites were consistently sampled and thus enabling comparison of data between comparable seasons. The eight most abundant or relatively consistently present mollusc species were used, *viz Acteocina* sp, *Arthritica semen, Bedeva paivae, Bittium granarium, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella* and *Tellina deltoidalis.*

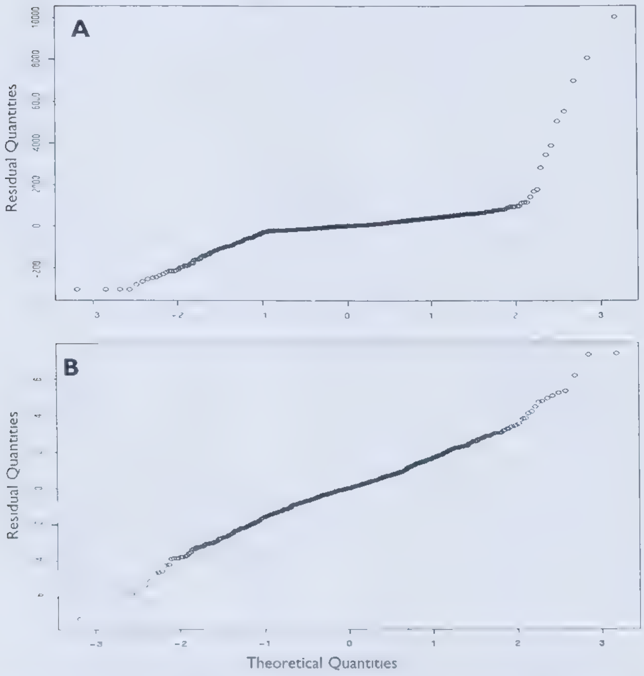

Figure 2. A: Residual analysis for untransformed mean occurrences of mollusc species. **B:** Residual analysis for Log Transformed Mean Occurrences

For the clustering analysis, the following information was used: each category of environmental parameter was assigned its actual numerical value, or where a parameter had a range of qualities or values, or to a class category: year (*e.g.* 1983); site (*e.g.* site B11); depth (actual field measurement); estuarine salinity field assigned to a class I = deltaic field, II = lower estuarine field, III = mid estuarine field, IV = upper estuarine field); % content of mud in the substrate (actual value); seagrass assigned to a class 0, 1 or 2; *Chaetomorpha* assigned to a class (0 = if absent, 1 = present but patchy, 2 = present and continuous or abundant); mollusc species (mean number of individuals in a square metre based on five replicates for each of the eight species sampled).

During data processing, since zero scores for abundances were inadmissible to the programme, specific sites and species, in which there were no biota for a given year, or the species were generally absent through the estuary for that year, respectively, were excluded. For 1983, data included *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for all sites, and *Acteocina* sp *Bittium granarium* were excluded. For 1984, data included *Acteocina* sp, *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for 21 sites, and *Bittium granarium* and site A1 were excluded. For 1985 data included *Acteocina* sp, *Arthritica semen, Bedeva paivae, Bittium granarium, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for 21 sites, and Sites A1 and D20 were excluded. For 1986 data included *Arthritica semen, Bedeva paivae, Hydrococcus brazieri, Nassarius burchardi, Spisula trigonella,* and *Tellina deltoidalis* for all sites; *Acteocina* sp and *Bittium granarium* were excluded.

Results

Abundance trends

Analysis of the mean occurrences of molluscan fauna clearly indicates significant two-way interactions between species and times, as well as species and sites, but not between times and sites. Due to the significant two-way interactions, little can be said about the significant main effects. The model accounts for approximately 50% of the variation. The analysis of standardised residuals (Fig 2) showed departures from normality where the variation increases with the mean value, indicating that a logarithmic transformation of the data should be undertaken. Table 1 presents the results of the full analysis of transformed data, where all the two-way interactions are significant and the model accounts for 73% of the variation of the data. The log residual analysis (Fig 2) indicates a much closer alignment with the underlying normal distribution assumptions of the model. There are still a small number of residuals, which are either under, or over-estimated by the model and which may require closer investigation.

Using the log transformed data, further analyses highlights the trends in time and/or salinity and their effects on the mean occurrences of the species.

Table 1. Results of the analysis of log transformed mean occurrences

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	67.2***
times	10	240.5	24.05	4.9***
sites	11	648.8	58.98	11.9***
species x times	60	571.4	9.52	1.9***
species x sites	66	2422.3	36.70	7.4***
times x sites	85	544.9	6.41	ns
Residual	472	2337.4	4.95	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

The results of the analysis of site groups are presented in Table 2. This analysis shows highly significant (< 0.1%) two-way interactions between species and site class with significant (5%) interactions for species by time and site class by time. The model accounts for approximately 55% of variation in the data.

Table 2. Results of the analysis of mean occurrences with grouped site classes

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	48.9***
times	10	240.5	24.05	3.5***
site class	3	271.1	90.37	13.3***
species x times	60	578.0	9.63	1.4*
species x site class	18	1373.9	76.33	11.2***
times x site class	28	321.8	11.49	1.7*
Residual	585	3980.0	6.80	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

The species by site class interaction indicates that the mean occurrences of species vary significantly with the site class. That is, some species are more prevalent at some of the site classes than others, showing in the along-estuary trend, some species are influenced by the salinity field gradient and might well be more salt-tolerant than others that are found further up the estuary.

The analysis of linear trend in site classes, using the indicator values (A -> 1, B-> 2, C -> 3, and D -> 4) is shown in Table 3. A significant positive (or negative) trend parameter would indicate that there is a gradient dependent on site class - that is, a salinity trend up (down) the estuary.

Table 3. Results of analysis of linear trends of grouped site classes

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	41.9***
times	10	240.5	24.05	3.0***
linear site trend	1	15.5	15.50	ns
species x times	60	579.7	9.66	ns
species x site trend	6	897.4	149.57	18.9***
times x site trend	10	136.7	13.67	ns
Residual	617	4895.4	7.93	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ ns = not significant.

Table 3 illustrates a highly significant trend for species by linear site *i.e.* for individual species the trend across the estuary varies. Some species react more to the gradient in the salinity fields than others, with decreasing or increasing mean occurrences changing up (or down) the estuary. There are still significant differences between species and time.

The results of the analysis of linear time and site class trends, simplified by reducing the 10 degrees of freedom for time to a linear trend over time are shown in Table 4. Time has been "ordered" to indicate either a positive (or negative) linear trend, reflecting increases (or decreases) in overall species occurrences over the sampling time. Interactions, especially of species with time, would indicate that species occurrences are not consistent across time(s) *i.e.* some species may decrease over time while others remain stable or even increase.

Table 4. Results of analysis of linear trends of grouped site classes and time

Source	Df	Deviance	Mean Deviance	F
species	6	1996.5	332.75	41.1***
time trend	1	105.1	105.10	13.0***
site trend	1	15.9	15.90	ns
species x time trend	6	162.0	27.00	3.3**
species x site trend	6	893.3	148.88	18.4***
time x site trends	1	10.0	10.10	ns
Residual	689	5579.0	8.10	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

This analysis indicates significant species by time and species by site class interactions. A further analysis which included a polynomial trend term for time indicated that the polynomial trend term is non-significant for time and can be eliminated from the model. The other significant interactions of species by linear time trend and species by linear site trend are still present.

The results of the final linear model includes the main effects of species, time trend and site class trend with interactions of species with time trend and species with site class trend (Table 5). No other effects have been included. In this model, all effects except the main effect of site classes are significant.

Table 5. Final analysis of occurrences

Source	Df	Deviance	Mean Deviance	F
NULL			8761.70	
species	6	1996.5	332.75	41.1***
time trend	1	105.1	105.10	13.0***
site trend	1	15.9	15.90	ns
species x time trend	6	162.0	27.00	3.3**
species x site trend	6	893.3	148.88	18.4***
Residual	690	5589.0	8.10	
Total	**710**	**8761.8**		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

The trends of abundance of the individual species over time using the final linear model are shown in Figs 4 & 5, with log-transformed predicted species abundance shown. for the four hydrochemical settings within the estuary in time. Fig 4 shows the patterns for the February data from each year, and Fig 5 shows the similar patterns for the May data. The patterns evident for each of the species are different in detail, showing variation in the rate of decrease or increase in overall populations numbers in time, and exhibiting small to large changes in abundance along the south to north estuarine gradient. *Acteocina* shows a very slight increase in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Arthritica* shows an evident decrease in relative abundance throughout the whole estuary in time, and there also is a small but consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Bedeva* shows a slight decrease in relative abundance throughout the whole estuary in time, and there is a relatively small but consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Hydrococcus* shows a very slight decrease in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites. *Nassarius* shows a clear decrease in relative abundance throughout the whole estuary in time, and there is a very large and consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Spisula* shows a very marked decrease in relative abundance throughout the whole estuary in time, and there is a large and consistent contrast in abundance from south to north, with the species consistently more abundant in southern sites. *Tellina* shows a moderate decrease in relative abundance throughout the whole estuary in time, and there is a moderate and consistent contrast in abundance from south to north, with the species consistently more abundant in northern sites.

Clustering

The similarity/dissimilarity of the molluscan fauna sets derived from Flexible UPGMA Method for the years 1983-1986 shows the same patterns as described above. That is, predominately year to year variation in associations of mollusc species, with separations on the dendrogram for the different species occurring variably from year to year (Fig 5). However, there are three low-level associations: *Nassarius* and *Tellina* are associated in 1983, 1985 and 1986, though not 1984, separating on the similarity/dissimilarity axis at about 0.4 to 0.6; *Hydrococcus* and *Bittium* are weakly associated in 1984; and *Hydrococcus* and *Bedeva* are associated in 1986.

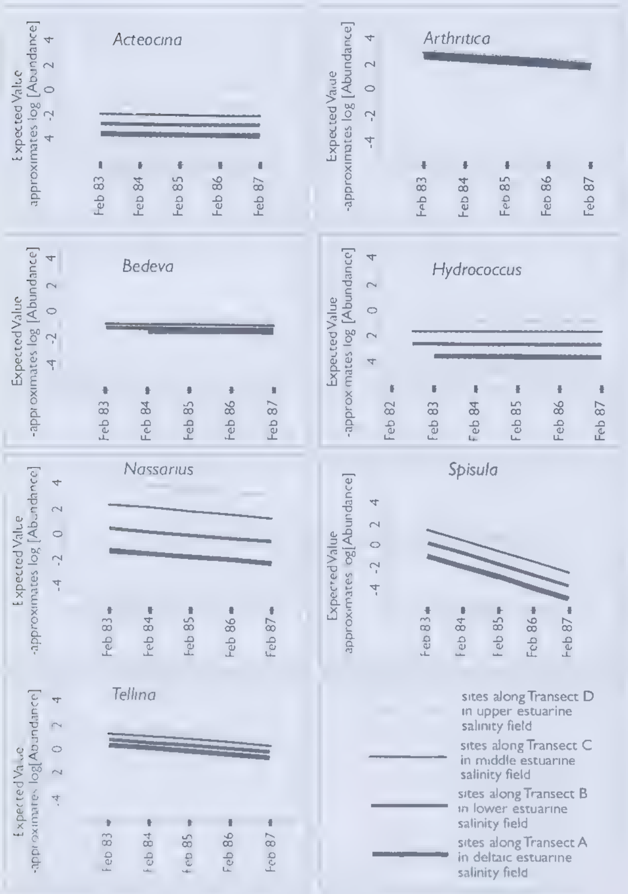

Figure 3: Graph of site class by time interaction for *Acteocina, Arthritica, Bedeva, Hydrococcus, Nassarius, Spisula* and *Tellina* for the sampling period February 1982 to February 1987. X-axis is time. Y-axis approximates log of abundance.

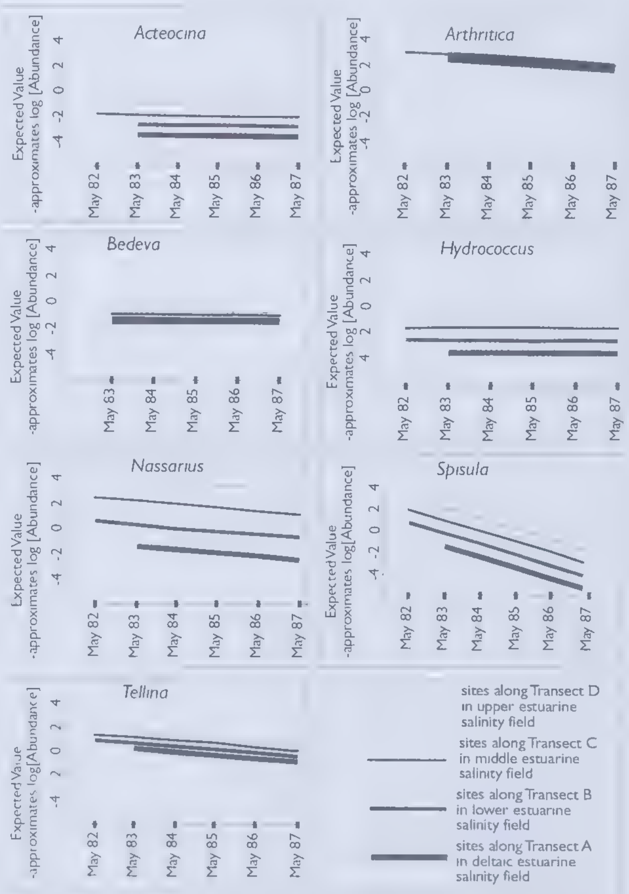

Figure 4: Graph of site class by time interaction for *Acteocina, Arthritica, Bedeva, Hydrococcus, Nassarius, Spisula* and *Tellina* for the sampling period May 1982 to May 1987. X-axis is time. Y-axis approximates log of abundance.

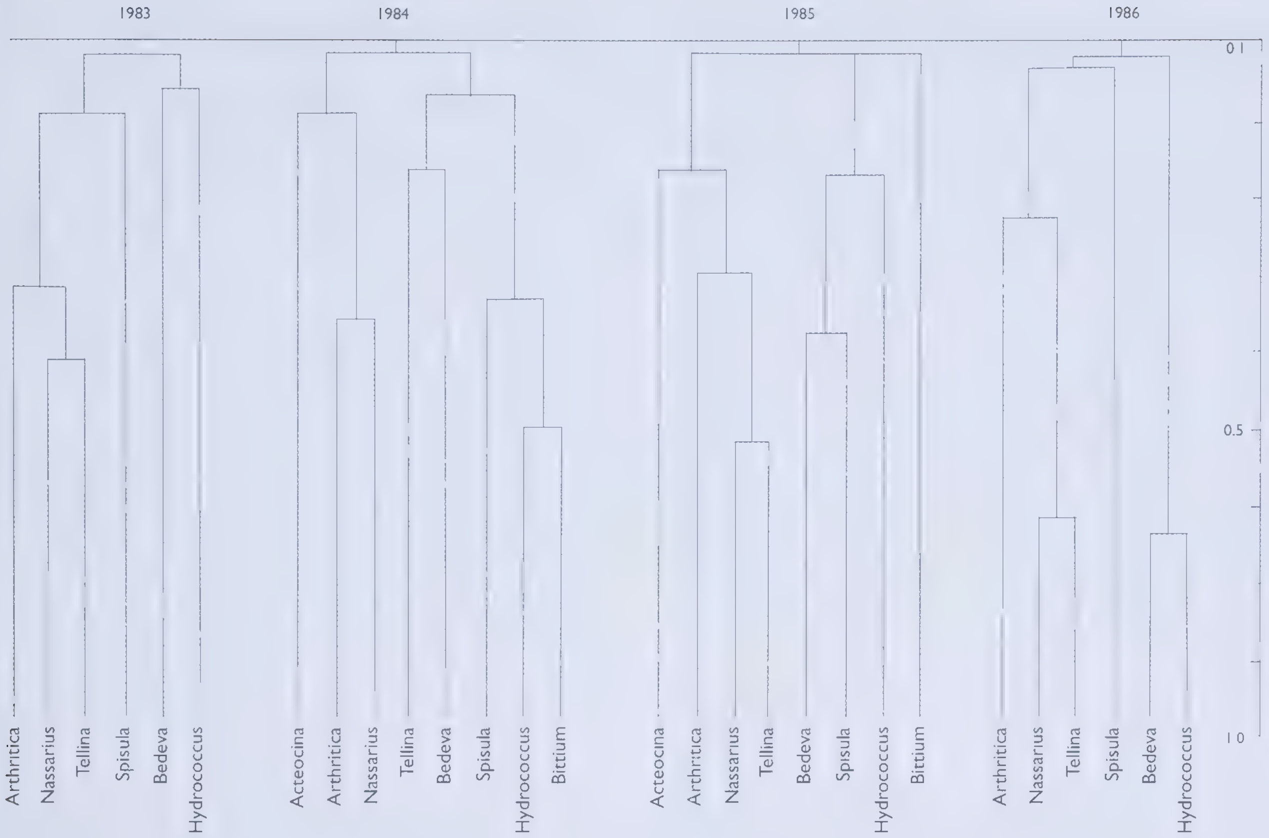

Figure 5. Dendrogram using Flexible UPGMA Strategy, for individual years between 1983-1986.

Discussion

Note should be made here that since only the February and May data were processed for each year, effectively using data from the summer months when the south to north gradient is at its most pronounced in terms of a transition from marine to hypersaline, the fluctuations in populations numbers brought about by freshwater and temperature effects are eliminated. The trends in the graphs thus illustrate an underlying pattern in the population numbers. Also, patterns derived from data for both February and May each year are similar.

Our analyses of mollusc abundance trends, both spatially and temporally, had an objective of summarising the responses of the various species as succinctly as possible to interpret the species responses. This has been achieved by looking for trends within time and/or sites (response to the south to north salinity gradient in the estuary) for each species. The final linear model does not account for as much variation in the data as more complex models but provides a simple interpretation of the responses.

The hydrochemical setting with its south to north gradient provides a framework to interpreting species distribution. While allocation of sampling sites to estuarine salinity fields reflects a gradient of increasing salinity, with A being marine to freshwater, B being mainly marine, and C and D reflecting a wider salinity fluctuation with salinities becoming progressively more saline and hypersaline for parts of the hydrologic cycle, the gradient also may reflect other changes in hydrochemistry in the estuarine waters, in that nutrient content and turbidity may be linked to fluvial influx and bathymetry of the estuary. However, for purposes of this paper, the hydrochemical gradient is considered to be the main factor, and in the discussions that follow the gradient from south to north in the estuary is referred to as the "salinity gradient".

The analysis of species by times by sites clearly indicates there to be significant time and/or site trends within the data (the latter reflecting the hydrochemical gradient, or salinity). These trends are significantly species-specific, which is to be expected since some species are more marine in character and opportunise the estuary during appropriate times of the hydrochemical cycle, than others. Some species respond to both time and salinity (site) levels while other species may show only a response to either time or salinity gradient, but not both.

Almost all of the species show an effect of site or salinity (*i.e.* location in the prevailing estuarine salinity field), but this varies markedly between the species. *Arthritica* and *Bedeva* show a minimal difference or effect of site (salinity), and only small decreases in mean count over time. However, *Spisula* and *Tellina* show much larger effects of changes over the gradient and over time, with *Spisula* being strongly influenced by the prevailing salinity gradient. This effect of location within the estuary, related to the salinity gradient may be due to the prevailing gradient in salinity, or nutrient content, or some other expression of the hydrochemical field, *e.g.* phytoplankton), or combinations of these (Semeniuk &

Wurm 2000). Progressing along the estuary from A to B, C and then D, there is a marked decrease in the mean count for these two species, reflecting their preference for more marine conditions, and potential intolerance of hypersaline conditions. There is also a marked decrease in counts, for all sites, over the time of the study, a factor that related to the overall long-term population dynamics of the species in response to longer-term patterns of estuarine environments (*e.g.* increase or decrease in nutrient enrichment, or volumes of freshwater influx on a 20-year cycle, amongst others).

The relationship between location (salinity) and abundance described above is also evident for *Nassarius*. However, for this species the decline with time is much less noticeable than for *Spisula*. *Tellina*, on the other hand, shows the reverse trend for site. The mean counts increase as the salinity level increases up the estuary. Again, there is a decrease in the mean count over the term of the study, but this decline in count over time is much less noticeable that the decline associated with *Spisula*. The final two species, *Acteocina* and *Hydrococcus* have site responses similar to *Arthritica*, but only very small response to time.

In summary, the seven mollusc species can be assigned to two groups on the basis of their responses to the south to north gradient along the estuary:

1. The first group consists of *Arthritica*, *Acteocina*, *Hydrococcus* and *Tellina*; which has had a positive response to the south-to-north gradient. The level of this response varies markedly between the four species, with *Arthritica* exhibiting almost no differences between sites, *Tellina* exhibiting a larger between-site effect, whereas *Acteocina* and *Hydrococcus* show marked effects of site differences. *Arthritica* and *Tellina* indicate a decrease over time whereas the other two species show little if any effect of time.
2. The second group consists of *Bedeva*, *Nassarius* and *Spisula*; which has a negative response to the south-. to-north gradient. The mean counts decrease markedly, especially for *Nassarius* and *Spisula* as salinity increases. *Nassarius* and *Spisula* have marked time effects with counts decreasing over time. There is only a slight trend in time for *Bedeva*.

These contrasts in temporal and spatial patterns will result in varying assemblages at a given time. That is, given there are positive *vs* negative trends of abundance for the different species along the south to north estuarine gradient, as well as decreases *vs* increases in abundance in time, and different rates of change (rapid decrease *vs* negligible decrease), it follows that assemblages determined by the present/absence, and relative abundance of the principal species of mollusc will be highly variable from year to year.

The dendrogram shows year to year changes in abundance of mollusc species such that different aggregation of species would result from data used at one particular time to that used from another. For example, the assemblage groupings arising from data for February 1983 are different to those arising from data for February 1984. This would indicate that researchers must exercise caution in using results from one year, or even several years, to categorise biotic assemblages mathematically within environments such as estuaries that exhibit a marked level of hydrochemical and biotic dynamism. Our conclusion is that the attempt to categorise the mollusc fauna mathematically in "assemblage" failed largely because there are no clear associations. The most marked and consistent association appear to be for *Nassarius* and *Tellina*, but this association was not consistent for all years.

One of the interesting features to emerge from these mathematical analyses is that the results of the spatial and temporal analyses of abundance could be used from first principles to derive the various assemblages with their variable faunal compositions from year to year. This would indicate marked intra-assemblage variability from year to year, patterns that are evident and corroborated by the dendrogram. Overall, it would seem that mathematical and cluster analyses of biotically dynamic systems should be confined to autoecological analyses until the larger holistic patterns are well understood.

The crucial factors underpinning the inter-annual variability in faunal "communities" is the dynamic nature of the estuarine environment. Aspects of variation in habitats temporally influencing biotic assemblages and changing species associations in time are explored and discussed by Austin (1985). For the Leschenault Inlet estuary, there are changes in estuarine hydrochemistry from year to year (reflecting, for instance, inter-annual and inter-decadal rainfall variability in the environment and in the catchment, and variable loading of anthropogenic nutrient). There is inter-annual variability in hydrodynamics, driven by wind and storms (affecting sediment transport and sedimentation). There is variability in the population dynamics of primary producers (with influx and intra-estuarine dispersion of floating marine algae, the growth and contraction of seagrass beds, the increase and decrease in plankton) and its concomitant effects on epibenthic and infaunal biota), and variability in the recruitment, migration, mortality rates, of benthos.

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Appendix 1. Mean abundance of mollusc species per metre square for the various sites and times used in this study

	A2	A3	A4	B9	B11	B12	C15	C17	C19	D20	D21	D22
Acteocina												
Feb-82	*	*	*	0	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	170	0	0	0
Feb-83	0	0	0	0	0	0	9.6	0	0	9.6	3.2	13
May-83	0	0	0	0	0	*	0	0	0	3.2	3.2	*
Feb-84	0	0	0	0	0	0	58	0	38	19	13	90
May-84	0	0	0	0	0	*	3.2	0	45	26	9.6	9.6
Feb-85	0	0	0	0	0	0	16	0	32	0	32	22
May-85	0	0	0	0	0	*	0	0	0	0	0	6.4
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0
Feb-87	0	0	0	0	0	*	0	0	0	106	67	112
Arthritica semen												
Feb-82	*	*	*	*	*	*	*	*	*	*	*	*
May-82	0	0	127	1529	510	0	662	1885	25	51	1885	255
Feb-83	3159	0	76	688	0	0	917	4637	*	3159	16052	127
May-83	892	0	178	408	51	*	1248	1885	*	382	*	*
Feb-84	178	0	382	382	102	0	2675	357	408	1987	7924	1223
May-84	0	0	0	535	0	*	0	0	*	229	994	1554
Feb-85	51	0	102	178	306	0	0	0	0	0	153	0
May-85	1147	408	280	0	153	*	153	153	*	1172	815	917
Feb-86	51	204	51	76	0	0	229	255	0	0	127	0
May-86	204	153	25	96	25	0	76	280	0	0	127	0
Jan-87	5657	1987	1350	764	1198	*	917	2548	*	2370	10217	484
Feb-87	76	357	0	1427	0	*	0	4383	*	11415	13606	0
Bedeva paivae												
Feb-82	*	*	*	1.6	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	6.4	3.2	0	0	0
Feb-83	0	9.6	0	6.4	0	0	3.2	3.2	0	0	0	0
May-83	9.6	0	0	0	0	*	0	13	0	0	0	*
Feb-84	0	35	0	0	0	0	3.2	0	0	0	0	0
May-84	0	0	0	0	0	*	0	3.2	3.2	0	0	0
Feb-85	0	3.2	0	32	0	3.2	0	0	6.4	0	0	0
May-85	6.4	0	0	3.2	0	*	0	0	0	0	0	0
Feb-86	0	0	0	3.2	0	0	0	0	0	0	0	0
May-86	0	0	0	9.6	0	0	0	0	0	0	0	0
Jan-87	0	3.2	0	6.4	3.2	0	0	3.2	0	0	0	0
Feb-87	3.2	0	0	16	0	*	6.4	0	0	0	0	0
Hydrococcus brazieri												
Feb-82	*	*	*	0	*	0	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	3974	0	0	0
Feb-83	0	0	0	0	0	0	6.4	0	15008	9.6	3.2	0
May-83	0	0	0	0	0	*	0	0	0	0	3.2	*
Feb-84	0	0	3.2	3.2	0	0	0	0	0	3.2	9.6	6.4
May-84	0	0	0	0	0	*	99	0	32	0	3.2	0
Feb-85	0	0	0	0	0	0	0	0	0	0	0	0
May-85	0	0	0	0	0	*	32	0	9.6	0	38	6.4
Feb-86	0	0	0	0	0	0	3.2	0	0	0	0	0
May-86	0	0	0	0	0	0	9.6	0	0	0	0	0
Feb-87	0	0	0	0	0	*	0	0	109	35	3.2	3.2
Nassarius burchardi												
Feb-82	*	*	*	93	*	6.4	*	*	*	*	*	*
May-82	154	32	486	77	29	42	32	6.4	0	0	0	0
Feb-83	285	250	1446	387	211	198	32	154	0	0	0	0
May-83	474	256	1338	374	93	93	19	51	0	0	0	*
Feb-84	3.2	74	938	381	32	38	45	115	0	0	0	0
May-84	9.6	16	301	35	64	*	0	26	0	0	0	0

Appendix 1 (continued). Mean abundance of mollusc species per metre square for the various sites and times used in this study

	A2	**A3**	**A4**	**B9**	**B11**	**B12**	**C15**	**C17**	**C19**	**D20**	**D21**	**D22**
Nassarius burchardi												
Feb-85	32	22	3.2	387	61	22	3.2	80	0	0	0	0
May-85	22	19	13	42	42	*	0	70	9.6	0	0	0
Feb-86	9.6	0	42	48	6.4	*	0	9.6	3.2	0	0	3.2
May-86	74	0	6.4	202	9.6	*	9.6	9.6	9.6	0	0	6.4
Feb-87	6.4	26	42	154	38	*	38	74	3.2	0	0	0
Spisula trigonella												
Feb-82	*	*	*	1.6	*	3.2	*	*	*	*	*	*
May-82	570	512	0	0	6682	11958	0	13504	45	0	0	0
Feb-83	1222	2326	0	0	5570	4384	0	2880	42	0	0	0
May-83	1107	2774	3.2	0	3456	3296	0	1760	35	0	0	*
Feb-84	0	1078	0	0	38	3.2	0	0	0	0	0	0
May-84	9.6	0	0	0	0	*	0	0	0	0	0	0
Feb-85	0	3.2	3.2	0	3.2	3.2	0	0	0	0	0	0
May-85	9.6	0	0	0	0	*	0	0	0	0	0	3.2
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0
May-86	6.4	0	0	0	0	0	0	0	0	0	0	0
Feb-87	3.2	0	0	0	0	*	0	0	0	0	0	0
Tellina deltoidalis												
Feb-82	*	*	*	59	*	94	*	*	*	*	*	*
May-82	0	29	83	80	48	154	61	58	3.2	0	35	0
Feb-83	0	22	166	198	77	102	70	86	0	6.4	13	6.4
May-83	3.2	6.4	154	123	48	*	38	80	3.2	3.2	6.4	*
Feb-84	0	6.4	266	96	80	83	83	90	0	26	3.2	0
May-84	0	0	102	6.4	77	*	32	96	0	64	6.4	9.6
Feb-85	0	67	106	70	138	67	13	118	6.4	0	18	22
May-85	0	0	32	6.4	0	*	0	6.4	0	26	0	0
Feb-86	0	0	32	38	16	67	0	0	3.2	9.6	42	67
May-86	0	0	29	19	3.2	61	13	0	0	26	45	61
Feb-87	0	3.2	83	154	38	*	38	74	3.2	16	0	3.2
Mar-87	0	6.4	80	125	45	58	106	29	6.4	13	3.2	0

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Small benthic Crustacea of the Leschenault Inlet estuary

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Abstract

Twenty-one species of small benthic and epibenthic crustaceans were recorded for the Leschenault Inlet estuary over the period 1982-1997. Two are new species, and eight species are probably new records for Western Australia. The most abundant species were *Tanais* sp nov and *Corophium* sp. Small benthic crustaceans had both widespread and restricted distribution patterns within the estuary. Spatial distributions of species appear to be linked to salinity patterns or to the presence of aquatic vegetation, and a few species also showed preference for particular substrates or depths. Summer and winter distributions varied. Changes in population density and distribution were likely linked to adult migration and juvenile recruitment. Over the five-year monitoring period, small benthic crustacean populations typically showed a seasonal unimodal peak in numbers during summer. This juvenile recruitment resulted in summer population densities typically an order of magnitude greater than winter densities. Less common species showed monthly to seasonal patterns that are difficult to interpret due to their sporadic occurrence in samples. The summer recruitment magnitude for most species varied annually, thus recruitment appears to be linked to favourable environmental conditions. A long-term environmental change within the Leschenault Inlet estuary was documented over this five-year period through the overall decline in abundance of the main species and through changes in species composition.

Keywords: benthic crusteans, Leschenault Inlet, estuary, south-western Australia.

Introduction

There have been few previous studies of small benthic crustaceans from Leschenault Inlet estuary or other estuaries of south-western Australia. Chalmer & Scott (1984) documented a number of small crustaceans as part of their fish and benthic fauna survey of the Leschenault Inlet estuary. In their study, the Leschenault Inlet estuary was sampled on a single occasion at three main localities: the inlet, central basin and northern flat of the estuary. They recorded three genera of amphipod, one species of isopod, and five decapods (mostly shrimps). Deeley (*pers. comm.* 1999 School of Environmental Science, Murdoch University) recorded small crustaceans from benthic samples collected along a north-south transect of Leschenault Inlet estuary, noting four amphipod taxa although only one was identified to species level. Hodgkin & Clark (1987-1990) compiled inventories of small benthic crustaceans from south-western Australian estuaries and coastal lagoons, listing a total of three amphipods, one talitrid (unidentified), one isopod and six decapods (mostly shrimps). Some records of small benthic crustaceans also were available from the crustacean database of the Western Australian Museum of Natural Science. These studies provide only an indication of species found in south-western Australian estuaries on single sampling surveys, without replication in time or in space. In this paper, I provide an inventory of species compiled from data collected seasonally over five years at 22 sites within the estuary, and address spatial and temporal changes in abundance and composition of key species over this time.

Methods

Regional setting

Leschenault Inlet estuary is a north-south elongate basin with rivers located at its southern end. The marine access channel also is located at the southern end through an artificial cut (V Semeniuk, 2000). The position of the mouth and head of this estuarine system generates a nonlinear gradation in salinity and substrate types from lower to upper reaches. Although the range of salinity within the basin is within estuarine conditions, the variability of salinity in different sections is atypical in comparison with classic estuaries described by Day (1981).

The Leschenault Inlet estuary was subdivided into habitat and hydrochemical sectors by Wurm & Semeniuk (2000). Four divisions are recognised on the basis of salinity; upper, mid, lower-estuarine and deltaic regions. This subdivision provides a framework within which to interpret distribution patterns of benthic fauna. Wurm & Semeniuk (2000) and Semeniuk (2000) describe physical, chemical and sedimentological aspects of Leschenault Inlet estuary in some detail. Descriptions of salinity, substrate type, and aquatic vegetation are only briefly reiterated here to provide a context for the sampling sites (Fig 1). Salinity regimes are described after the Venice system for brackish waters (Anon, 1959).

Sampling of benthic fauna was undertaken along four cross-inlet transects, noted A-D (Fig 1). Biomass samples of the seagrass *Halophila ovalis* and algae were collected in 1986. Records of vegetation recorded along transects is provided below. Transect A (sites A1-7) is located mostly within the deltaic salinity field; water is typically

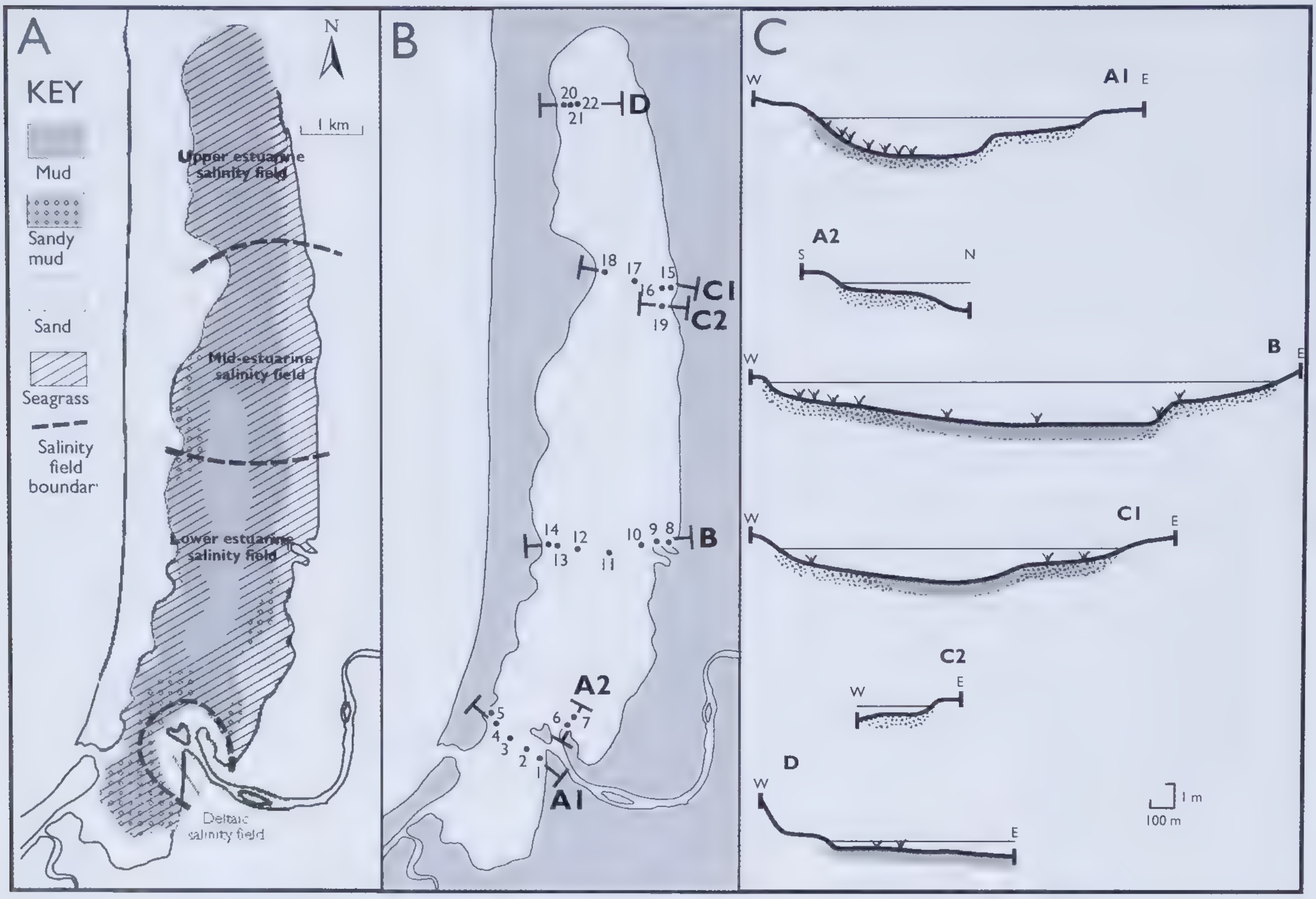

Figure 1. A: Habitat framework for Leschenault Inlet after Wurm (1987) showing salinity fields and main substrate types with superimposed distribution of seagrass species *Halophila ovalis* after Lukatelich (1993). B: Sampling sites. C: Detail of habitats along the four east-west transects after Wurm (1987). Seagrass records are from 1986 sampling trips and are marked at sampling sites only.

mesohaline in winter at sites A1-2 and A6-7, euhaline in winter at sites A3-5 and euhaline in summer at all sites (salinity range per annum is typically 15-40 ‰). Substrates are generally sandy with sandy mud in the central zone of the estuary, corresponding to the deeper basin area (sites A4 and A5). Sites A3-5 had *Halophila* present (sites A1-2 and A6-7 are located on the delta front and had no seagrass present). Algae were present at sites A5-7. Transect B (sites B8-14) is located in the lower-estuarine salinity field; water is euhaline throughout the year (salinity range per annum is 35-40 ‰). Substrates grade from sand on the eastern margin to mud in the deeper basin region (sites B11 and B12), and to sandy mud on the western margin. *Halophila* was present at all sites. Algae occurred only on the western margin at sites B13 and B14. Transect C (sites C15-19) is located in the mid-estuarine salinity field; water is euhaline throughout the year, but fluctuates within this category at shallow-water sites C15-16 and C18-19 (salinity range per annum is 30-45 ‰). Substrates grade from sandy mud on the eastern margin to mud in the deeper basin region and western margin. Both *Halophila* and algae occurred along the shore margins at sites C15, C16, and C18. Transect D (sites D20-22) is located in the upper-estuarine salinity field; water is hyperhaline in summer and polyhaline in winter (salinity range per annum is 25-60 ‰). Sites are located in the intertidal zone and hence experience a more extreme seasonal temperature range than other sites in the estuary. Temperature range is 15-30 ° C per annum. Substrates are typically muddy with patchy algal cover.

Methods

Small benthic and epibenthic crustaceans were collected on surveys of Leschenault Inlet estuary between February 1982 and May 1987. Fauna samples were first collected on a reconnaissance survey in February 1982, when ten replicate samples at a total of 26 sites were collected. Sampling was continued seasonally along the four transects described above between May 1982 and May 1987. On these later surveys, five replicates at each of the 22 sites were collected.

In addition, five samples were collected monthly at eleven of the above sites (sites A2, A3, A4, B9, B11/12, C15, C17, C19, D20, D21 and D22) from June 1986 to May 1987 to provide more detailed information on population dynamics of fauna species along these transects. A total of 3025 samples were collected. Samples were collected in August 1997 at each of the sites A4, C15 and D22 to provide additional specimens for taxonomy.

The scope of spatial and temporal replication in samples throughout the estuary provides an important benthic data-base for estuarine environments. These samples are used to determine species distribution within the estuary and to assess the significance of habitat associations within the framework described by Wurm & Semeniuk (2000). The time scale over which the samples were collected gives an indication of species response to the fluctuating physical and chemical conditions in this estuary. Abundance and species composition are analysed on a seasonal to annual basis, and also over the five-year period.

The sampling method used in this study was designed specifically for smaller benthos. However, epiphytic and nektonic species were commonly recorded at vegetated sites because animals were trapped in collected vegetation.

Benthos was collected by randomly taking cores, 10-cm diameter and 15-cm deep, from the sediment surface. Thus, a 78.5 cm^2 surface area was excavated to 15 cm depth. This ensured 95% probability of collecting organisms with living densities greater than 0.06 specimens dm^{-3} (Dennison & Hay 1967). Spatial replication meant that a total of *ca* 400 cm^2 was investigated at each site on each sampling trip. This ensured 95% confidence of collecting species with densities as small as 0.009 specimens dm^3 (Dennison & Hay 1967). Abundance of individual species is given in this paper as specimens per sample for the purpose of comparison of fauna densities between sites and species. This avoids errors induced by assuming constant density or no small-scale heterogeneity when extrapolating to larger areas. Specimens per sample can be converted to specimens per m^{-2} by multiplying by a factor of 127.

Sediment and any surface vegetation was removed and washed over a 1 mm sieve in the field. Fragments of menthol were added to samples containing polychaetes immediately after collection, as part of the collecting procedure for associated polychaetes. Initially, sieved residue was decanted into bottles, fixed in formaldehyde, re-washed and then stored in 10% phenoxytol solution. Benthos was picked from the residue in a laboratory at a later date. Specimens were analysed in 1996-1997. Samples were collected in 1997 to provide fresh material for taxonomic work.

Taxonomic reference standards were established using the expertise of J Lowry and B Wilson at the Western Australian Museum, and the following literature: Hale (1927-1929), Barnard (1969, 1972), Barnard & Karaman (1991), and Poore & Lowry (1997). Specimens were sorted and counted from each sample. A total species list was compiled from these data for the Leschenault Inlet estuary. Additional records from 1997 were added to the list.

The nature and scope of the Leschenault Inlet estuary environmental surveys emphasised the collection of information on habitats, sedimentology, molluscan fauna, and general other benthic fauna. There was no specific focus on collecting and preserving small benthic crustaceans. In contrast to the preservation methods outlined above, ideally, samples for small benthic crustaceans should have been sieved over a mesh finer than 1 mm, and specimens picked in the field. Also, ethanol would have been a better storage medium, since failure to remove all formaldehyde and menthol contributed to deterioration of some material in a small number of samples (Gatanby & Beams 1950). However, comparison of reference standards with older material enabled identification of most specimens in these instances.

To evaluate distribution of species within the Leschenault Inlet estuary and to assess habitat associations, species are classified as very common (>20 specimens per sample), common (5-20 specimens per sample) and uncommon (0-5 specimens per sample) based on modal data from the sampled sites. Species distribution maps are provided for the most common small benthic crustacean species within the Leschenault Inlet estuary.

Sites representing shallow-water sand and mud, and deep-water mud habitats are considered in detail. These sites are selected to show the transition from lower to mid-estuarine salinity fields in the central basin muds (A3, B12 and C17) and shallow-platform sands of the western margin (B9 and C15). The northern flat site, D22, represents the shallow-water muds of the upper salinity field.

Results

Species inventory

A total of 21 benthic and epibenthic species of small crustaceans were recorded for the Leschenault Inlet estuary in this study (Table 1). Fifteen species were recorded over the period 1982-1987, with an additional six species recorded from 1997 samples. Eight species probably represent new records for Western Australia, based on a search of the Western Australian Museum of Natural Science records; however, two taxa are new species; *Tanais* sp nov and *Grandidierella* sp nov (J Lowry, Western Australian Museum, *pers. comm.*). *Paranthura* sp may also be a new species, since no similar specimens of this family are lodged at the WA Museum.

Table 1. Species list of small benthic crustaceans for Leschenault Inlet

Species	Life mode
AMPHIPODA	
Austrochiltonia subtenuis	epibenthic
Amphitoe cf kulafi ledoyer	epibenthic
Amphitoe ngana	epibenthic
Amphitoe cf valida	epibenthic
Amphitoe sp	epibenthic
Caprella cf penantis	epibenthic - nektonic
Corophium sp	benthic
Ericthonius pugnax	benthic
Grandidierella sp nov	epibenthic
Grandidierella japonica	epibenthic
Melita zylandica kauerti	epibenthic
Melita matilda	epibenthic
Melita sp	epibenthic
Paracorophium excavatum	benthic
Tethygeneia elanora	epibenthic
ISOPODA	
Tanais sp nov	benthic
Sphaeroma quoyanum	benthic
Paranthura sp	benthic
DECAPODA	
Ebalia intermedia	benthic
Halicarcinus ovatus	benthic
Illyoplax sp	benthic

The most abundant small benthic species were *Corophium* sp, and *Tanais* sp nov. Specimens of *Caprella cf penantis, Paranthura* sp, *Melita zeylandica kauerti* and *Melita matilda* also were regularly recorded in the samples. Other species were recorded only rarely, or only in 1997. Only species with average specimen totals greater than one per sample will be discussed further. These are *Corophium* sp, *Tanais* sp nov, *C. cf penantis, Paranthura* sp, and *Melita zeylandica kauerti.*

Diversity

Overall species diversity for this estuary was low. Samples typically contained between 1-3 species. Highest diversity was recorded along Transect A: basinal sandy mud site A3 and platform muddy sand site A4 typically had eight species present. Diversity decreased slightly from Transect B in the lower-estuarine region to Transect C in the mid-estuarine region, from around six to four species per site, and then increased to seven species per site along the upper-estuarine Transect D.

Highest diversity thus occurred in the regions with close to normal marine salinities and stable temperatures. High diversity also occurred in the regions of greatest salinity and temperature fluctuation *i.e.* the upper-estuarine reach and the deltaic region. Lowest diversity correlated with the mid-estuarine field, which had higher than normal marine salinities and relatively stable temperatures.

Spatial patterns

Distributions of small benthic crustacean species within the estuary were either widespread or restricted (Fig 2). Abundance data for individual species for each site are presented in Table 2. Density patterns within the estuary are described below for each of the key species.

Tanais sp nov was widespread within the Leschenault Inlet estuary. It was recorded at all 11 sites that were monitored monthly. High numbers of specimens were recorded at most shallow-water sites; B8-9, C15-16, C18-19, and D21-22. The species was more abundant at shallow-water sites on the eastern and northern margin, where there were population densities of up to 150 specimens per sample in summer.

Corophium sp also was widespread within the Leschenault Inlet. It was recorded at all of the 11 sites monitored monthly, occurring with highest frequency in the Collie Delta region at site A2. High frequencies also were recorded at lower-estuarine basin site A3 and mid-and lower estuarine shallow sandy sites B9 and C15 along the eastern estuary margin. At these sites population densities were up to 100 specimens per sample in summer. *Corophium* sp was recorded in much lower numbers along Transect D, where sample densities were typically 1-2 specimens per sample. This species had a widespread distribution within Leschenault Inlet estuary.

Paranthura sp similarly was widespread, and recorded at all 11 sites that were monitored monthly. However, it occurred most commonly within the mid-estuarine salinity field. Summer distributions typically extended into both the upper and lower estuarine salinity fields. Highest densities were recorded at basin and platform sites with muddy substrates; densities were up to 13 specimens per sample in summer. The distribution pattern within Leschenault Inlet estuary was restricted.

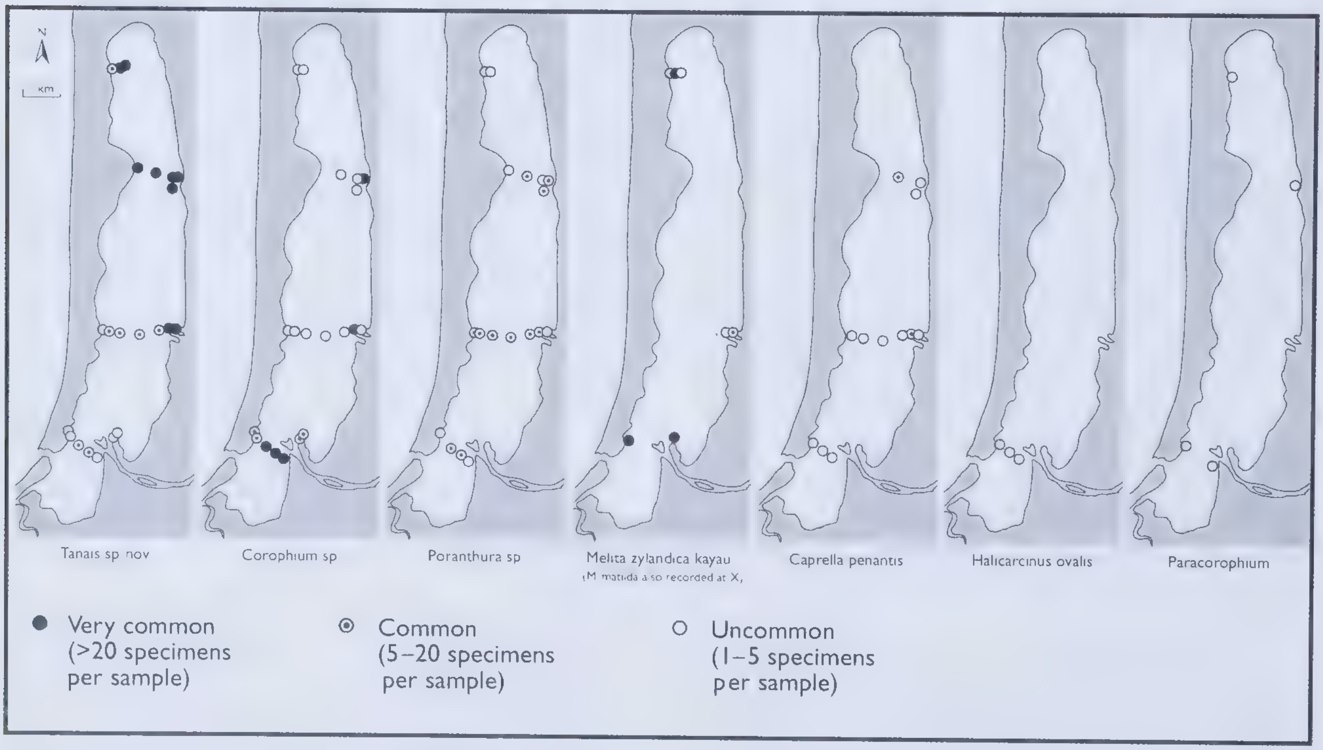
N
km
Tanais sp nov
Corophium sp
Poranthura sp
Melita zylandica kayau
(M matilda also recorded at X)
Caprella penantis
Halicarcinus ovalis
Paracorophium
● Very common (>20 specimens per sample)
⊙ Common (5–20 specimens per sample)
○ Uncommon (1–5 specimens per sample)

Figure 2. Species abundance at monitored sites based on maximum abundance recorded between 1982-87. This gives an indication of net distribution within the estuary, but does not represent occurrence at a given time, since abundance varied seasonally and annually at sites.

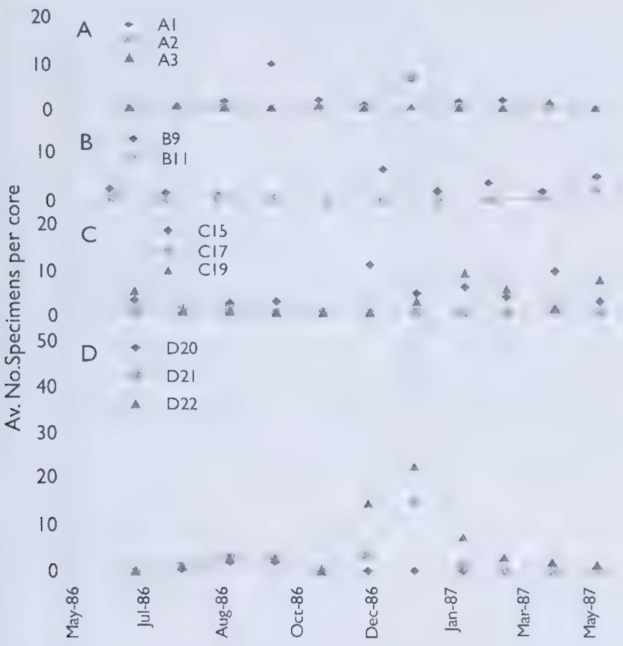

Figure 3. Monthly change in mean abundance of *Tanais* sp nov at monitored sites along the four Transects (A-D) over the period May 1986 to May 1987 (mean and standard deviation is calculated from five sample replicates collected each month at each site).

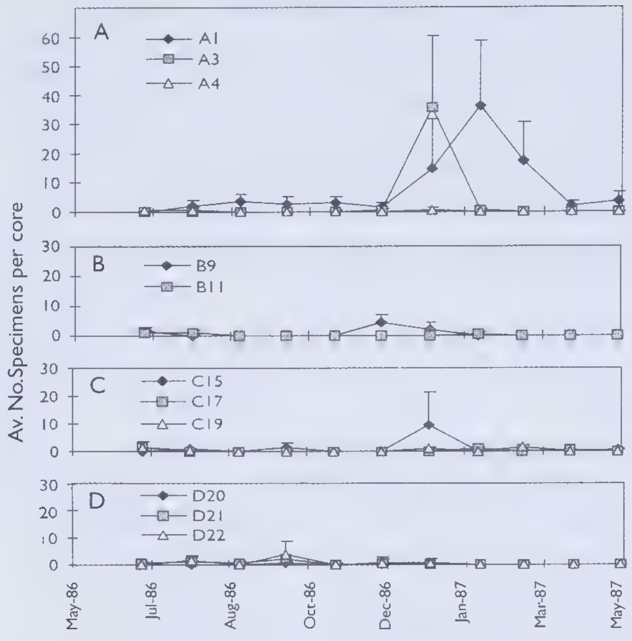

Figure 4. Monthly change in abundance of *Corophium* sp at monitored sites along the four Transects (A-D) over the period May 1986 to May 1987 (mean abundance and standard deviation calculated from five sample replicates collected each month at each site).

Caprellid shrimps and most amphipods were recorded mainly from vegetated sites. *C. cf penantis* was generally recorded from seagrass substrates along Transects A-C (within the lower to mid-estuarine salinity fields) at sites A3, A5, B9, B10-11, and C16-17 of the sites monitored monthly. It was recorded most frequently and with highest numbers at sites A3, B9-10 which correlates with high density of aquatic vegetation. It typically occurred at densities of 1-7 specimens per sample. Summer and winter distributions of *C. cf penantis* varied slightly: the summer distribution was more widespread within the estuary and it was recorded more frequently along Transect A. There were few records of this species from Transect D. This species was confined to regions with close to normal marine salinities within the estuary.

Melita spp were recorded from nearshore sites along Transects A, B and D. *M. zeylandica kauerti* was most frequently recorded. Summer and winter distributions of *M. zeylandica kauerti* varied slightly: it was recorded year-round at Collie Delta and northern flat sites, but was only recorded at mid-estuarine nearshore sandy sites B8-10 in summer. *M. zeylandica kauerti* occurred at densities of up to 3 specimens per sample. *M. matilda* was recorded only during summer in 1984 and 1986 from sites A4, A7, B8, B10, and D21. Both species of *Melita* had restricted distribution patterns within Leschenault Inlet estuary.

Small crabs, especially *Halicarcinus ovatus,* were recorded along Transect A at sites A2-4. These sites are located in the lower-estuarine salinity field, in muddy sands from deeper water regions of the central basin. Small crabs were recorded rarely; their distribution patterns were very restricted within Leschenault Inlet estuary.

Other crabs (*e.g. Ebalia* and *Illyoplax*) and most amphipods (*e.g. Amphitoe, Grandidierella, Ericthonius, Tethygeneia*) were too rare to establish distribution patterns. However, amphipods from the genera *Amphitoe* and *Grandidierella* were typically recorded in algae-rich samples.

Temporal patterns of species

Analysis of the 1986/87 data collected at monthly intervals indicates that the three most abundant species typically recruited in summer (Figs 3-5). Monthly to seasonal changes in abundance of less common species is difficult to interpret due to their sporadic occurrence in samples.

The number of specimens of *Tanais* sp nov increased in summer at most of the sites that were monitored, with the exception of deeper water basin sites A4, B11, C17 and intertidal site D20 where numbers remained steadily low (Fig 3). The highest average number of specimens was recorded at sites D21 and D22, where numbers changed from an average of 0-2 specimens per sample up to 30 specimens per sample in December to January. Similarly, all shallow-water to intertidal sites along Transects A, B and C that were monitored monthly showed an increase from an average of 0-2 specimens per sample to around 13 specimens per sample in December to January. Brood eggs attached to crustacean specimens were observed in many samples collected during December to April. Two recruitment phases were recorded at site B9 during this period: an earlier phase in October 1986, and one in the December to January period. Sporadic occurrences of egg-bearing specimens also were noted in August and October each year at a number of sites. Hence, recruitment was not confined to the summer period.

Summer recruitment also was observed in *Corophium* sp populations at some sites (A1, A3, B9 and C15). How-

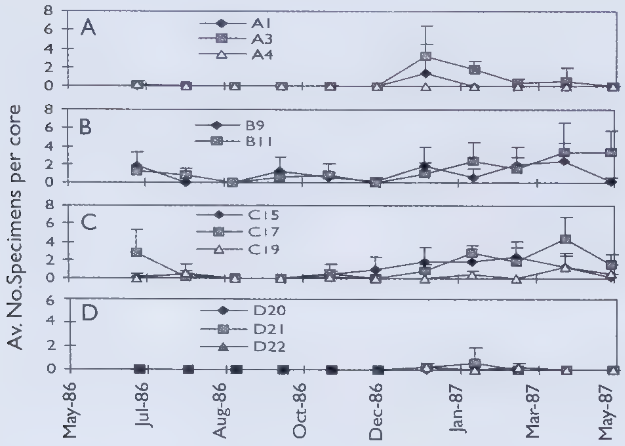

Figure 5. Monthly change in abundance of *Paranthura* sp at monitored sites along the four Transects (A-D) over the period May 1986 to May 1987 (mean abundance and standard deviation calculated from five sample replicates collected each month at each site).

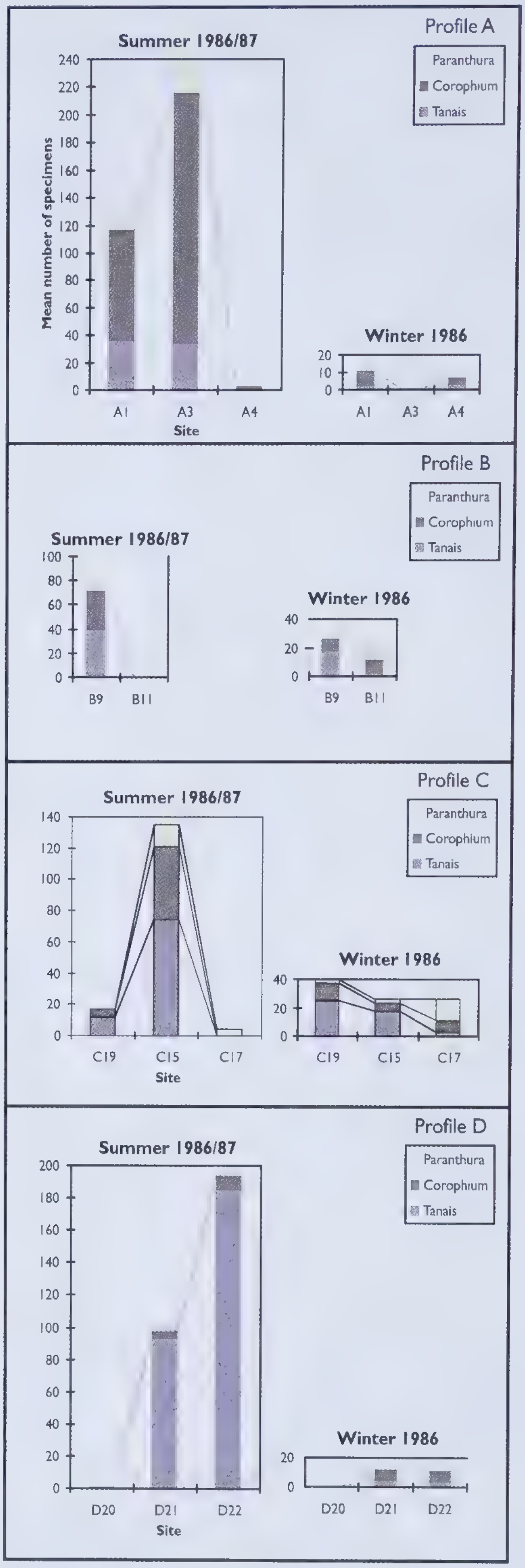

Figure 6. Summer and winter sample compositions for 1986/87 at monitored sites along the four east-west Transects (A-D). Summer compositions are based on total species counts from December 1986 and January 1987. Winter compositions are based on total species counts from June 1986 and July 1986.

ever, the majority of sites monitored monthly had consistently low numbers of specimens throughout the year. The shallow lower-estuarine reaches had the largest density changes over the summer where densities changed from a steady average of 0-2 specimens per sample up to 36 specimens per sample in January (Fig 4).

Paranthura sp was not commonly recorded in samples, hence it is difficult to establish reliable population patterns. Highest numbers were recorded from deep-water basin sites. It occurred along Transects B and C sporadically throughout the year, however peak numbers were recorded during January to March. The species was only recorded along Transects A and D during January to March (Fig 5).

The remaining species were not common enough to analyse for monthly to seasonal temporal patterns, although a number of trends can be discerned. *C. cf penantis* was more often recorded in summer months between December and February than at other times. *Melita* spp were recorded along Transect D and A in summer and generally only recorded along Transect D in winter.

Seasonal to annual population variation

Seasonal variation in composition and abundance of populations occurred along all transects over the five-year sampling period. Differences between winter and summer samples are illustrated by comparing winter 1986 and summer 1986/87 data for *Tanais* sp nov, *Corophium* sp and *Paranthura* sp (Fig 6). Four distinct seasonal trends were observed at different sites within the estuary. An increase in density of all three species was observed at sites B9 and C15. An increase in density of only one species was observed at sites A1, A3, D21 and D22, whereas no changes in density were observed at sites A4 and C19 and a decrease in density of species was observed at sites B11 and C17. Individual species patterns are described for each transect below.

Transect A Samples along Transect A showed a marked change in numbers and a change in proportions of the three species *Tanais* sp nov, *Corophium* sp and *Paranthura* sp at sites A1 and A3, but no change in numbers at site A4. Sites

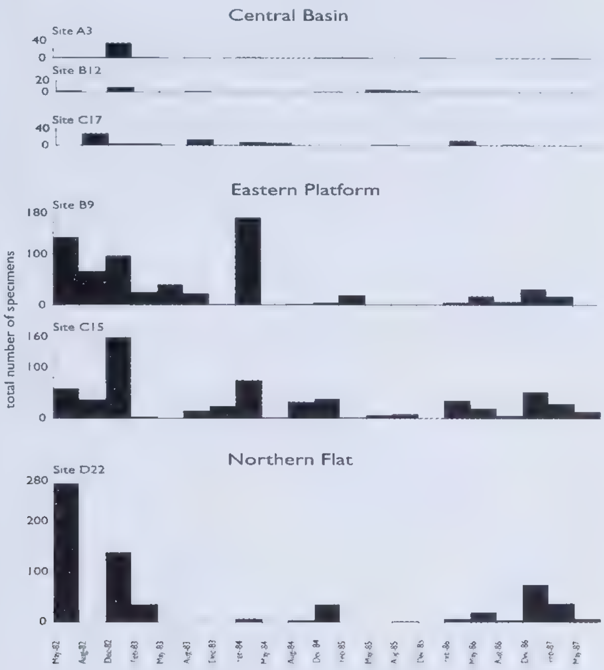

Figure 7. Long term annual changes in density of *Tanais* sp nov from seasonal data collected between May 1982 and May 1987. Total species counts from five replicate samples are given for each sampling occasion at each site. Sites are chosen to show population trends along the length of the estuary for deep-water and shallow-water regions.

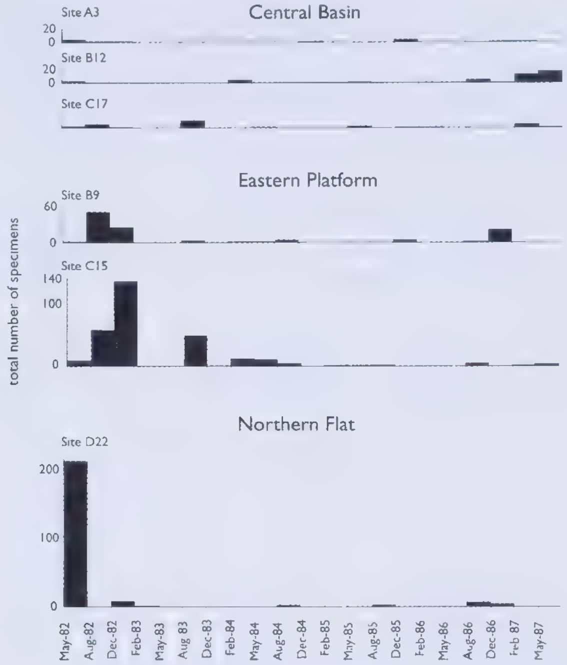

Figure 8. Long term annual changes in density of *Corophium* sp from seasonal data collected between May 1982 and May 1987. Total species counts from five replicate samples are given for each sampling occasion at each site. Sites are chosen to show population trends along the length of the estuary for deep-water and shallow-water regions.

A1 and A3 showed two orders of magnitude increase in density of *Corophium* sp, compared with a one order of magnitude increase in density of *Tanais* sp nov. *Paranthura* sp was only recorded in summer.

Transect B Sites B9 and B11 showed completely different seasonal trends. In winter, composition and abundance were similar between sites, however, numbers of all three species (*Tanais* sp nov, *Corophium* sp and *Paranthura* sp) doubled at site B9 in summer, whereas all specimen numbers decreased at site B11 (except for *Paranthura* sp).

Transect C Sites along Transect C showed similar trends for these species to those already described for Transect B: site C17 showed the same trends as site B11, site C15 was similar to site B9 and samples from site C19 showed no seasonal change in density.

Transect D Sites D21 and D22 showed two orders of magnitude increase in density of *Tanais* sp nov, whereas the density of *Corophium* sp remained constant. Site D20 showed no significant density changes.

Annual and long-term trends also are best illustrated by individual species. Figs 7 and 8 respectively show the total numbers of specimens of *Tanais* sp nov and *Corophium* sp at six selected sites over the five-year sampling period. These sites represent shallow-water sand and mud, and deep-water mud habitats within the estuary. Population peaks at sites A3, B12 and C17 are compared with salinity, temperature and oxygen saturation records collated by Wurm & Semeniuk (2001).

Tanais sp nov recruited mainly in December to February. Specimen numbers peaked markedly at sites A3, B9, C15 and D22 in December 1982 and at sites B9 and C15 in February 1984. These represent maxima within the five-year period of sampling. The major recruitment peak in summer of 1984 followed a polyhaline period at sites A3, B11 and C17 (which most probably affected the whole estuary in the winter of 1983). Recruitment peaks at site C17 also post-dated polyhaline periods. Peaks of lower magnitude occurred over the summer at sites B9, C15 and D22. Total numbers appeared to decline at most sites over the period 1984 to 1987, despite recurrent recruitment (Fig 9).

Corophium sp recruited mainly in the period August to December, but sometimes also in the period February to May. Specimen numbers peaked at sites B9, C15 and D22 between May and December 1982. The next highest peaks in populations at these sites occurred in August to December 1986. Total specimen numbers, however, declined dramatically between these recruitment periods. Peaks of lower magnitude occurred in August 1983, February 1984, August to December 1985 and 1986 at some of these sites. Recruitment was seasonal at some sites and intermittent at others. Peaks in population densities at sites A3, B12 or C17 do not correlate with seasonal patterns observed for salinity, temperature or oxygen.

Habitat associations

Wurm & Semeniuk (2000) recognised at least twenty-one habitat types within the Leschenault Inlet estuary. Fourteen of these habitat types were sampled regularly on benthic surveys of the estuary. Species abundance with respect to these habitats indicates some possible habitat associations (Table 2).

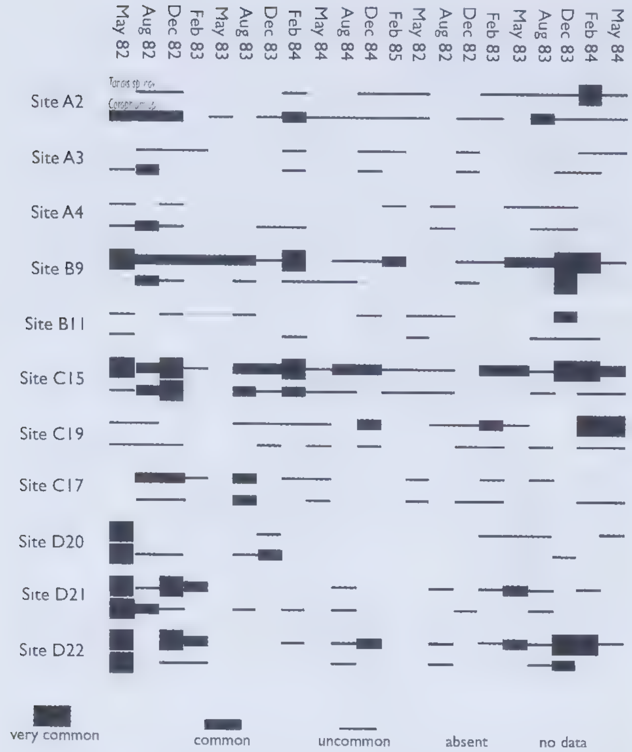

Figure 9. Long term changes in species occurrence at all 11 monthly monitored sites over the five-year period, May 1982 to May 1987. Abundance is rated as very common to rare based on the number of specimens recorded at each site.

While *Tanais* sp nov was an ubiquitous species occurring in all salinity fields, and nearly all habitats, it was distinctly less common at sites in the lower-estuarine field. Although there was no indication of salinity or substrate preference, the species appeared to prefer the higher temperatures or higher levels of oxygen found in shallower waters. Distribution information from other estuaries would be required to establish whether this species is a euryhaline marine or true estuarine species.

Corophium sp inhabited sandy habitats in mid to lower estuarine fields. Since it is also recorded from many other south-western Australian estuaries (Hodgkin & Clark 1987-1990; WA Museum of Natural Science crustacean database) this suggests it is a euryhaline opportunist or a true estuarine species.

Paranthura sp inhabited muddy sand to mud habitats in the mid to lower-estuarine fields. It is likely a euryhaline marine species, but distribution information from other areas would be required to confirm this conclusion.

Caprellid shrimps were recorded from most deltaic, lower and mid-estuarine sites within the Leschenault Inlet estuary, with the exception of sites in the most northern parts of the estuary. The shrimps were most common at vegetated muddy sand and mud basinal sites in the lower to mid-estuarine salinity field, generally at sites where salinities were close to normal marine conditions. A restricted distribution pattern within the Leschenault Inlet estuary is typical of stenohaline marine species with low tolerance for hyperhaline or polyhaline salinities. This species has both marine and estuarine records from Western Australia (WA Museum of Natural Science crustacean database).

Melita spp were restricted to intertidal and nearshore platform margin sites on the Collie river delta and northern intertidal flat. Both areas had variable salinity, including mesohaline periods. *Melita* spp within Leschenault Inlet estuary may have been associated with freshwater mixing zones along the estuarine margin and deltaic areas, since they were not recorded from all shallow-water nearshore sites. Both *Melita* spp were originally described from south-western Australian estuaries (Barnard 1972) and frequent records of *Melita* sp occur for many south-western Australian estuaries (Hodgkin & Clark 1987-1990), hence both are probably true estuarine species or euryhaline opportunists.

Small crabs were recorded from the Collie River Delta and central basin sites only. These genera were associated with lower-estuarine basinal sands and sandy muds with close to normal marine salinities. The numerous marine records of these small crab species from Western Australia suggest that they are stenohaline marine species (WA Museum of Natural Science crustacean database).

Some differences in the abundance of species occurred between sites representing the same habitat which suggest factors other than substrate and salinity play a role in determining species distributions (Table 2). *Tanais* sp nov was very common at lower-estuarine platform muddy sand site B9, but uncommon at sites A4, B10 and B13; very common at mid-estuarine muddy sand site C15, but not at site C16; common at deltaic intertidal sand site A1 and upper-estuarine intertidal mud site D22, but not at deltaic intertidal sand sites A6, A7 or upper-estuarine intertidal mud site D21. Environmental factors other than salinity, temperature and substrate may affect densities (*e.g.* oxygen saturation, depth or wave energy) and determine the shallow-water preference of *Tanais* sp nov. Alternatively, food source may be a factor.

Corophium sp, *Melita* spp and *Paranthura* sp showed only minor differences in abundance between sites representing the same habitat: *Corophium* sp and *Melita* spp were common at site B9, but not at A4, B10 or B13. This suggests site B9 may have environmental attributes which separate it from other lower-estuarine platform muddy sand sites *e.g.* the combination of shallow depth and nearshore wave energy may generate a different oxygen environment. It also has a higher seagrass biomass than most other sites along Transect B.

Most crustacean species present in the estuary may be regarded as euryhaline marine species or euryhaline opportunists, since the salinity range within the estuary is from 15-60 ‰. Some stenohaline marine species also are present, but do not occur in the polyhaline regions of the estuary. Freshwater species were not recorded because oligohaline to limnetic regions of the estuary only occur along the Preston and Collie river channels and were not sampled in this study.

Discussion

Estuarine environments typically have variable chemical and physical environmental conditions. Fauna assemblages reflect environmental heterogeneity in an instant in time along a coenocline, and through time at a given

Table 2. Abundance of crustacean species with respect to the habitat framework of Wurm & Semeniuk (2000)

Habitat	**Site**	*Tanais* sp nov	*Corophium* sp	*Paranthura* sp	*Melita zeylandica kauerti*	*Caprella cf penantis*
deltaic region intertidal sand salinity: mesohaline in winter; euhaline in summer	A1	*	**	**	*	-
	A6	*	**		-	
	A7	*	*		*	
deltaic region sand salinity: mesohaline in winter; euhaline in summer	A2	***	***	**	-	-
lower estuarine platform intertidal muddy sand salinity: euhaline	A5	*	***	-	*	*
lower estuarine platform muddy sand salinity: euhaline	A4	*	*	*	*	*
	B9	***	***	**	*	**
	B10	***	*	*	*	*
	B13	**	*	*	-	*
lower estuarine platform sand salinity: euhaline	B8	***	*	*	*	*
lower estuarine platform sandy mud salinity: euhaline	B14	*	-	**	-	-
lower estuarine basin sandy mud salinity: euhaline	A3	***	***	**	-	**
lower estuarine basin mud salinity: euhaline	B11	**	*	***	-	*
	B12	*	*			*
mid-estuarine platform intertidal sand salinity: fluctuating euhaline	C19	***	*	*	-	-
mid-estuarine platform sandy mud salinity: fluctuating euhaline	C18	***	-	*	-	*
mid-estuarine platform muddy sand salinity: fluctuating euhaline	C15	***	***	**	*	*
	C16	***	*	*	*	-
mid-estuarine basin mud salinity: euhaline	C17	***	*	**	-	**
upper estuarine intertidal sandy mud salinity: polyhaline in winter; hyperhaline in summer	D20	*	*	-	*	-
upper estuarine intertidal mud salinity: polyhaline in winter; hyperhaline in summer	D21	***	*	*	*	-
	D22	***	**	*	*	-

*** very common, ** common, * uncommon, - absent.

site due to fluctuating physical and chemical environmental conditions. A range of environmental factors, and especially salinity, appear to be first-order factors in determining species presence/absence at sites within this estuary. However, species distributions and densities exhibit recurrent temporal variation on seasonal to annual scales, probably caused by seasonal environmental changes and the intrinsic population dynamics of individual species. In addition, there is feedback between fluctuating environmental conditions and population dynamics because recruitment magnitude, juvenile and adult dispersal are all linked to favourable environmental conditions. Biological controls also could influence distribution patterns through species competition and predation. Temporal variation on decadal and longer time scales is likely linked to more dramatic shifts in environmental setting, such as nutrient enrichment, rather than to population response to fluctuating environmental conditions.

Without details on population size classes, reproduction, recruitment strategies, and information on a host of environmental factors, it is difficult to uncouple the biological from environmental processes that cause temporal variation in distribution and population density at a given site. Hence this discussion will first focus on net distribution patterns and then on changes to distribution and density of species on different time scales.

Faunal composition within this estuary does not reflect the typical lower to upper-estuarine faunal changes from marine to freshwater species found in most other estuaries (Day 1981; Kennish 1990). A longitudinal section across the Leschenault Inlet estuary shows a gradation in species between Transects A to D, in which the fauna components shift from euryhaline marine and stenohaline marine species to mainly euryhaline marine to mixed euryhaline species. However, this north to south pattern is disrupted at Transect A, which had euryhaline marine, estuarine opportunists and stenohaline marine components. There may even be a gradation in faunal composition, east to west, from river delta to Inlet, along Transect A. These unusual faunal patterns are attributed to the north-south oriented, elongated basin geometry and to the fact that the position of rivers in the Leschenault Inlet estuarine system generate atypical mid-estuarine and upper estuarine reaches. The mid-estuarine region does not have the classical polyhaline range in salinity and hence does not have the characteristic true estuarine components. The species composition in the "upper reaches" of this estuary (Transect D) is also highly uncharacteristic because it contains no oligohaline species. Species composition of the northern flat, in fact, is more analogous to coastal lagoon assemblages because this region experiences a hyperhaline period. Oligohaline species were found in the upper sections of rivers entering this estuary (Deeley, School of Environmental Science, Murdoch University, *pers comm.*), hence the true upper-estuarine salinity field of Kennish (1990) is located along the river channels adjacent to the lower-estuarine field. Thus, basin and river geometry accounts for the low number of stenohaline marine species and the absence of freshwater species recorded in the estuary proper, which contributes to a low overall species diversity.

Diversity patterns within the estuary reflect the complexity of environmental conditions within different estuarine fields. For instance, the highest diversity of small benthic crustaceans recorded along Transect A reflects the complexity of the juxtaposition of head and mouth of the estuary. Lowest diversity was recorded in the mid-estuarine field. Hence, the diversity pattern of the Leschenault Inlet estuary also differs from the typical estuarine pattern described by Kennish (1990) in which maximum diversity occurs in the mid-estuarine salinity field.

The distributions of the most common species of small benthic crustaceans were mainly widespread, but indicated some habitat associations. Tanaids were most abundant in well-oxygenated shallow areas of the northern flat, eastern and some western platform and deltaic sites even though habitats in these regions range from upper-estuarine intertidal mud to deltaic sands. *Corophium* sp was most common in deltaic to lower-estuarine platform sands, with the highest numbers recorded from the Collie Delta area; whereas *Paranthura* sp was most abundant in the mid to lower-estuarine muddy sand and mud habitats.

The common species from the melange of species within the various sites can be used to define four assemblage types within the estuary based on differences in the relative abundance of species. The deltaic region was characterised by high numbers of *Corophium* sp, with less common occurrences of other species including *Tanais* sp nov and *Melita* spp (the *Corophium-Tanais-Melita* assemblage). The mid to lower-estuarine regions had different shallow-water and deep-water assemblages; *Corophium* sp and *Tanais* sp nov dominated the shallow-water sites (the *Corophium-Tanais* assemblage), whereas *Paranthura* sp and *C. cf penantis* were found mainly in the deeper muddy sites (the *Paranthura-Tanais-Caprella* assemblage). Small crabs were found only in the lower-estuarine field at sites with close to normal marine salinities, hence the *Corophium-Tanais-Halicarcinus* assemblage only occurred at sites A3 and A4. The northern part of the estuary, the upper-estuarine field, was characterised by assemblages dominated by *Tanais* sp nov, with less common occurrences of *Melita* spp (the *Tanais-Melita* assemblage). Thus, assemblages could be distinguished from the following estuarine field and habitats; deltaic, lower-estuarine, near-shore lower to mid-estuarine, basin lower to mid-estuarine, and upper-estuarine. These assemblages appear to have been stable on seasonal to annual time scales.

Distribution of individual species based on presence/absence shows that most species are sensitive to at least one environmental variable. Those species found ubiquitously throughout the estuary showed density variation with respect to salinity and substrate, whereas those species that had restricted distribution showed correlation with salinity and vegetation. For example, salinity appeared to restrict the distributions of *Paranthura* sp, *Melita* spp, *C. cf penantis*, *H. ovatus* and other small crabs. In addition, the distribution of *C. cf penantis* was associated with the presence of vegetation within the mid to lower-estuarine salinity fields. This reflects habitat preference, but may also reflect some sampling bias since these mobile epiphytic crustaceans were more easily collected and trapped along with vegetation. The sample frequencies of *Corophium* sp and *Paranthura* sp show some correlation with substrate type within their distributions: *Corophium* sp had highest densities in sandy substrates whereas *Paranthura* sp appeared to prefer muddy substrates. Hence, a combination of substrate and salinity determined distributions of these two species within the estuary. The widespread shallow-water distribution of *Tanais* indicates that other important environmental factors, such as depth, oxygen saturation of the sediment, temperature or food source also played a role. Hence, distributions of the species were not always correlated to habitats defined on the physico-chemical and substrate criteria of Wurm & Semeniuk (2000). It is important to note that some environmental factors such as temperature and salinity varied on seasonal to annual cycles and hence would have affected distributions on these temporal scales, whereas other factors such as substrate are fixed constraints on distributions.

Seasonal changes in salinity and possibly other environmental shifts (such as oxygen and temperature) may contribute to transient changes in species distributions through their affect on adult migration and juvenile dispersal. Seasonal migration of adults probably accounts for changes in numbers of *C. cf penantis* and *Melita* spp at a number of sites. These species showed different summer and winter distribution patterns most likely linked to salinity changes, since temperature changes were fairly consistent for sites of similar depth throughout the estuary. For example, *Melita* spp were commonly recorded in the northern transect sites in winter and were less common in summer when the salinity regime shifted from meso

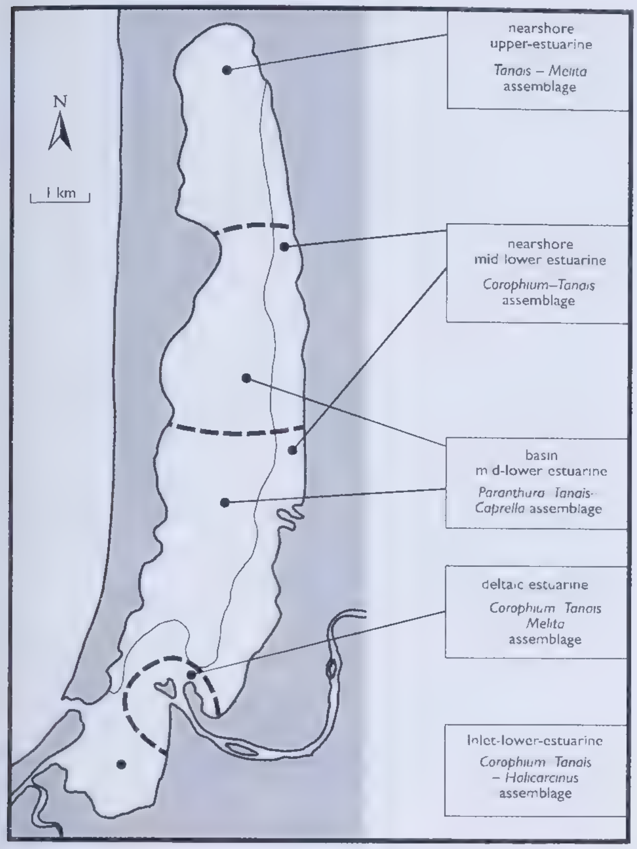

Figure 10. Distribution of small benthic crustacean assemblages. Four assemblages determined by salinity range and substrate types are defined for the Leschenault Inlet estuary; a deltaic estuarine assemblage, a basinal mid to lower-estuarine assemblage, a nearshore mid to lower-estuarine asemblage and a nearshore upper-estuarine assemblage.

to hyperhaline. In summer, *Melita* spp also were recorded from the Collie Delta region and a number of other shallow-water sites in the mid-estuarine reach.

Summer and winter distributions of species also varied seasonally due to juvenile dispersal. Extensive and widespread juvenile dispersal generally resulted in a given species extending beyond the distribution boundaries of the adult organism. For example, the more widespread summer distribution of *Paranthura* sp may have reflected juvenile dispersal. Juveniles probably disperse beyond the regions in which they can survive to maturity.

Temporal changes in population density at a given site were conspicuous, often involving changes in abundance of several orders of magnitude. Temporal changes in density could be discerned on monthly to seasonal scales (those linked to population dynamics) and also on annual to decadal changes (those linked to population adjustments to major shifts in environmental conditions).

Monthly and seasonal changes in density at a given site were probably linked mostly to recruitment. Summer recruitment peaks were typical for most species. Populations of *Tanais* sp nov, *Corophium* sp and *Paranthura* sp all peaked in density between December and February. Less common species were not recorded frequently enough to establish abundance changes through time.

The abundance data indicate that both *Tanais* sp nov and *Corophium* sp recruited preferentially in shallow to intertidal sites, since the greatest increase in density occurred at these sites. Spring to summer increase in density of these species at deeper water sites may be attributed either to a later, lower magnitude recruitment, or to adult dispersal due to local intra-species or inter-species competition. There was no evidence of juvenile dispersion from shallow sites to deeper water sites along the same transects. *Paranthura* sp recruited preferentially in deeper water at sites with close to normal marine salinities.

Monthly data showed that recruitment magnitude and timing varied on seasonal to annual scales. Annual recruitment of individual species did not always occur simultaneously at all sites throughout the estuary (Fig 9). Inhomogeneous recruitment resulted in different seasonal and annual trends for each species at each site. For example, differences in the magnitude and timing of recruitment occurred between shallow- and deep-water populations of both *Tanais* sp nov and *Corophium* sp. Magnitude and timing of recruitment may have been influenced by local temperature, salinity change or to food supply. Clearly, from the perspective of specimen numbers and recruitment patterns, central basin and western platform appear to have been the preferred shallow-water habitat for both species.

Annual to longer term abundance patterns over the period 1982-1987 suggest that regular, if not annual, recruitment occurred in summer for most species over this period. Both *Tanais* sp nov and *Corophium* sp showed seasonal recruitment over the five-year period at least at one site. *Tanais* sp nov appears to be a resident species because it has an annual periodic recruitment pattern at most shallow-water sites and some deep-water sites. Recruitment during the December to February period was variable in magnitude, probably dependent on year to year environmental conditions. Major peaks recorded after polyhaline periods may represent population response after severe winter mortality. *Corophium* sp had a regular, but not annual recruitment pattern only at some shallow-water sites. The aperiodic recruitment of *Corophium* sp suggests that this species was greatly affected by the fluctuating environmental conditions within the estuary. Both species appeared to behave independently, since recruitment was not necessarily coincident with other species, and there was no indication of an inverse recruitment relationship between species over the five-year sampling period.

Over the five-year period of sampling there was an overall decline in numbers of both the dominant species. *Tanais* sp nov numbers decreased at sites B9 and C15. These declines may represent a shift in environmental conditions within the estuary *e.g.* an increase in nutrients within the estuary system. Similarly, *Corophium* sp numbers at site C15 declined over the same period. The decline in numbers of *Corophium* sp is even more obvious when populations at other sites are considered: this species has only been recorded commonly from site B9 since 1982, and only sites A2 and C15 show regular recruitment patterns (Fig 9). The unexpected high numbers recorded at site B9 in December 1986 and at site B12 in May 1987 is evidence for aperiodic recruitment. The decline in population of this species is difficult to interpret: it may represent response to adverse environmental change or it may reflect the population dynamics of an estuarine opportunist (Kennish 1990). Comparison of 1982-1987 environmental data with the current status of the estuary would establish whether these declines are linked to environmental change or to long term population dynamics.

The range of new species recorded in 1997 that had not been previously recorded in the estuary is another indication of compositional change in the estuary. Comparison of crustacean records with Chalmer & Scott (1984) indicate that the species assemblage present in 1974 was similar in composition and abundance to 1982, whereas the samples from 1997, twenty three and fifteen years later, respectively, were significantly different. The record of species associated with algae, especially *Amphitoe* indicate change in aquatic vegetation density and distribution within the estuary. The increase in algae at sites A4, C15 and D22 in 1997 compared with 1982-1987, is most likely the result of nutrient enrichment.

There is evidence for a number of environmental changes in physical, chemical and ecological conditions over the last decade. For example, Lukatelich (1989) documented changes in seagrass density over the period 1984-1988, and Ruiz-Avila & Klemm (1993) reported large variability in water chemistry between years. Either of these factors could generate long-term changes in fauna characteristics.

One possible underlying cause of environmental change is increased nutrient enrichment of the estuary. The estuary was first reported as being mildly "eutrophic" in 1991 (Hill *et al.* 1991). Nutrient enrichment would result in a change in chemical conditions and in the composition of primary producers, *e.g.* an increase, then a decrease in seagrass density at most sites, an increase in seaweed at most sites, and a decrease in available oxygen in water and sediment columns. Hence, population dynamics would be complicated by ever changing environmental stress.

The change in species composition and decline in abundance of both dominant species is most consistent with an environmental shift over time, rather than with patterns arising from a large variability in local conditions between years. Such a shift appears to preclude favourable recruitment resulting in low density, "maintenance" populations. Such environmental change will result in an ongoing change in population composition and structure of benthic crustaceans within the Leschenault Inlet estuary over the long term, until environmental conditions stabilise.

Only four out of the 21 species of small benthic crustaceans recorded for the Leschenault Inlet estuary in this study were previously recorded by other authors (it is possible overlap is higher because many small benthic crustaceans remain unidentified from previous work). All small benthic species recorded by other authors were recorded in this study. Differences in total species number partly reflect differences in rigor of sampling and sampling methods, but also temporal changes in species composition of this estuary.

A subset of the total small benthic crustacean species list for the Leschenault Inlet estuary has already been recorded for other estuaries in south-western Australia, hence there are faunal similarities with other estuaries. However, regional comparisons cannot be discussed in detail, since this study indicates that seasonal and annual changes in estuarine crustacean fauna are marked. Thus, single surveys, as have been conducted to date, may not be representative of diversity or species composition of benthic crustacean communities in estuaries, and a more rigorous study of other estuaries would be required to establish valid regional patterns. It also means comparative studies must take into account the marked annual to decadal changes in species linked to physico-chemical environmental changes in estuaries over time.

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Biology of the blue swimmer crab *Portunus pelagicus* in Leschenault Estuary and Koombana Bay, south-western Australia

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Abstract

The blue swimmer crab *Portunus pelagicus* was sampled monthly in Leschenault Estuary and the marine embayment (Koombana Bay) into which it opens. The trends exhibited by density and size-frequency data are consistent with those previously recorded for this portunid in this estuary, implying that the spawning period, the timing of immigration and emigration, and the pattern of growth are similar each year in Leschenault Estuary. The monthly trends exhibited by the numbers and prevalence of ovigerous female crabs, together with previous data on the distribution of crab zoea, provide strong circumstantial evidence that *P. pelagicus* typically release their presumptive zoea in Koombana Bay, rather than in Leschenault Estuary, and that this occurs predominantly in mid-spring to late summer. Although a few 0+ recruits enter the estuary in the ensuing months, their numbers do not start to rise markedly until the following mid-to late spring, when salinities and water temperatures in the estuary are rising appreciably. At this time, the carapace widths (CW) of the majority of these crabs lie between 40 and 100 mm. During the ensuing months, the corresponding cohort increases greatly in both numbers and body size, with the result that, by the completion of their first year of life in January, the CW of many of its females and males have reached 97 mm and 84 mm, respectively, the size at which 50% of the corresponding sexes of *P. pelagicus* undergo a pubertal moult. These and other data demonstrate that *P. pelagicus* first spawn when they are approximately one year old. Although the abundance of crabs in Leschenault Estuary rises during spring and summer, that of particularly the older crabs subsequently falls precipitously during the subsequent winter months and early spring, when the crabs are *ca* 18-20 months in age and salinities and water temperatures undergo a marked decline. The pronounced decline in the abundance of crabs in the estuary in winter and early spring is accompanied by a conspicuous rise in their numbers in the shallows of Koombana Bay, indicating that the crabs, which had emigrated from the estuary, had entered the alternative habitats provided by that embayment. A substantial number of crabs are found in Koombana Bay throughout the year. The sex ratios of crabs in samples collected by different methods indicate that females tend to leave the estuary before males and that crab pots have a greater tendency to catch male crabs than female crabs. The catch and catch per unit effort of the commercial fishery for *P. pelagicus* in Leschenault Estuary is greatest in January and February. This reflects in part the fact that, during these months, crabs are particularly abundant and are starting to attain the legal minimum size for capture (CW = 127 mm). This feature, together with the predominance of undersized crabs in earlier months and the emigration of crabs from the estuary in winter, help account for the marked seasonality of the fishery for this portunid in this estuary. Furthermore, as water temperatures are at their maxima in summer, the crabs are likely to be particularly active at this time and thus also most susceptible to capture. In the Leschenault Estuary, *P. pelagicus* feeds mainly on slow-moving or sessile macrobenthic invertebrates, such as amphipods, polychaetes, and bivalve and gastropod molluscs, and also occasionally on gobies, and thus in this system it can be regarded as essentially a benthic carnivore.

Keywords: Leschenault Estuary, *Portunus pelagicus*, size and age compositions, sex ratios, spawning, size at first maturity, recruitment, commercial fishery, south-western Australia.

Introduction

The Leschenault Estuary, which is located between latitudes 33° 12' S and 33° 20' S on the lower south-west coast of Australia, contains a large lagoonal-like basin, which is 14 km long and between 1.5 km and 2.5 km wide and in most regions is less than 2 m in depth (Semeniuk & Meagher 1981). The main tributary, the Collie River, discharges into the southernmost region of this basin, opposite the point where the entrance channel of the estuary opens into the sea at the northernmost end of Koombana Bay.

The blue swimmer crab *Portunus pelagicus* is found in waters throughout the Indo-West Pacific (Stephenson 1962), and is often sufficiently abundant to form the basis of a substantial recreational and/or commercial fishery in some of the estuaries and coastal waters in that region, including those of Leschenault Estuary (*e.g.* Potter *et al.* 1983; Ingles & Braum 1989; Sumpton *et al.* 1989; Kailola *et al.* 1993; Jones & Morgan 1994; Sukumaran & Neelakantan 1996a). Meagher (1971) provided the first data on the biology of *P. pelagicus* in the Leschenault Estuary and Koombana Bay. He concluded that this portunid emigrates from the estuary into the bay in autumn and returns in spring, and that these movements are related to temperature differences between the estuary and the embayment. He also concluded that the females of *P. pelagicus* reach maturity within this estuary during their second year of life and then migrate out to sea, where the fertilised eggs are released and larval development occurs. Anon (1983), in contrast to Meagher (1971), concluded that (1) the migration of *P. pelagicus* into

Leschenault Estuary occurs in mid-summer rather than spring, (2) during the summer, a substantial number of blue swimmer crabs remain in Koombana Bay rather than entering the estuary and (3) the females of this portunid first breed during their first year of life rather than at the end of their second year of life. However, the studies of neither Meagher (1971) nor LeProvost *et al.* (1983) were carried out at frequent, regular (*i.e.* monthly) intervals in both Leschenault Estuary and Koombana Bay. Such frequent sampling is clearly required to resolve the conflicting views on the above aspects of the biology of *P. pelagicus* in these two water bodies

The aims of the present study were to sample both nearshore, shallow and offshore, deeper waters of Leschenault Estuary and Koombana Bay at monthly intervals over a protracted period to clarify the following; (1) the size composition and patterns of immigration, emigration and growth of *P. pelagicus* in Leschenault Estuary and the relationships between the trends exhibited by these variables and those displayed by salinity and water temperature, (2) the relationship between the assemblages of blue swimmer crabs in Leschenault Estuary and Koombana Bay, (3) the time of spawning and the relationship between the attainment of first maturity and the body size of this portunid, (4) the composition of the diet of *P. pelagicus* in Leschenault Estuary and whether this is influenced by body size, (5) whether the mesh size of crab pots influences the size composition of the crabs caught, and (6) the extent to which the commercial catch of *P. pelagicus* in Leschenault Estuary has varied over the years and changes throughout the year, and to elucidate the reasons for the latter changes. Where appropriate, the results of the present study are compared with those previously recorded for *P. pelagicus* in the Leschenault Estuary and also in Cockburn Sound and the Peel-Harvey Estuary, which lie elsewhere in Western Australian waters (Penn 1977; Potter *et al.* 1983), in order to help resolve conflicting conclusions regarding the biology of this portunid in this estuary.

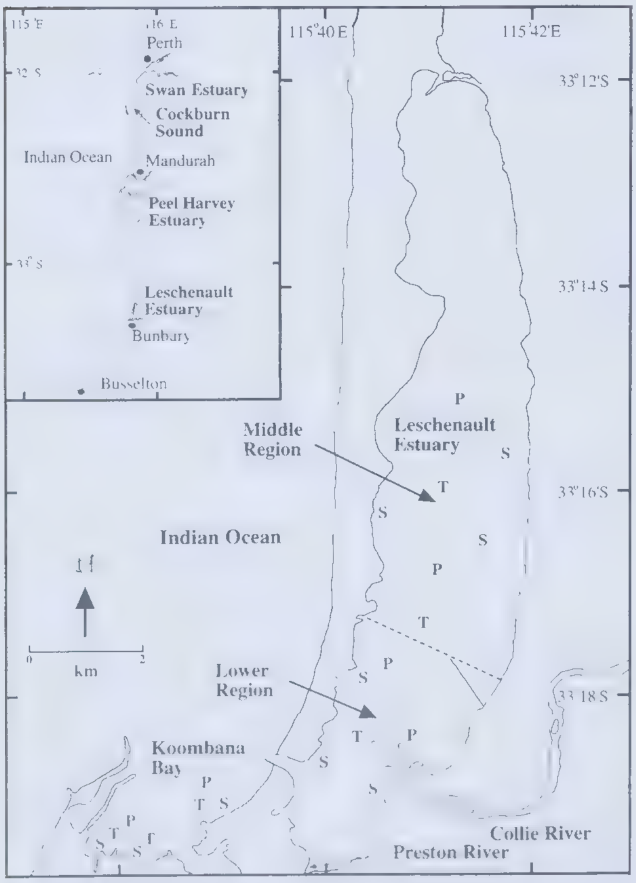

Figure 1. Map showing the sites in Leschenault Estuary and Koombana Bay that were sampled by seine nets (S), crab pots (P) and otter trawls (T). Inset shows location of Leschenault Estuary and Koombana Bay in south-western Australia.

Materials and Methods

Sampling

Portunus pelagicus was collected from sites in both nearshore, shallow (< 1.5 m in depth) and offshore, deeper waters (1.5-2.5 m) in the middle and lower regions of Leschenault Estuary and from nearshore, shallow (< 1.5 m) and offshore, deeper waters (5-7 m) in Koombana Bay (Fig 1). Shallow, nearshore waters were sampled by seine netting, whereas offshore, deeper waters were sampled using crab pots and an otter trawl. Sampling by pots and otter trawls could not be undertaken in the same depths in Koombana Bay as in Leschenault Estuary (*i.e.* 1.5-2.5 m) because in Koombana Bay those water depths coincided with the surf zone. Furthermore, otter trawling was not initiated until it became obvious that even pots with a small mesh size (12 mm) were not catching the small crabs that concurrent sampling for fish had shown to be present in offshore, deeper waters. The months in which sampling by seine netting, crab potting and otter trawling commenced were; Leschenault Inlet - seine nets in April 1996, crab pots in February 1996, otter trawls in June 1997; Koombana Bay - seine nets and crab pots in December 1996, and otter trawls in September 1997. In each case, sampling was carried out monthly until May 1998.

The seine net was 21.5 m long and consisted of two 10 m long wings, each comprising 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m long pocket consisting of 3 mm mesh. The net fished to a maximum depth of 1.5 m and sampled an area of *ca* 116 m^2. The catches of crabs obtained by seine net are expressed as a density, *i.e.* number of crabs caught per 100 m^2. On each sampling occasion, seine netting was carried out between 1 000 and 1 500 h at three sites in both the lower and middle regions of Leschenault Estuary and at three sites in Koombana Bay (Fig 1).

All of the 12 crab pots used on each sampling occasion were 630 mm high and 1000 mm in diameter. However, six of the pots were made of 12 mm mesh net, while the other six comprised 76 mm mesh. The 12 mm mesh, which was the strongest of the small meshes that were available, was chosen in an attempt to catch a full-size range of juvenile and adult crabs. The 76 mm mesh was selected as this mesh size is typical of that used by professional fishers in the Leschenault Estuary, Peel-Harvey Estuary and Cockburn Sound, and would thus provide a sample of crabs whose size composition would be similar to that obtained by commercial fishers. All pots were baited with fish. On each sampling occasion, four pots were joined together at

15 m intervals to produce a row of pots, in which the pots with the large mesh alternated with those with the small mesh. The remaining eight pots were then connected in the same manner to create two more rows, in which pots with the large mesh likewise alternated with those with small mesh. On the first night, a row of pots was placed randomly in each of three of the four crab pot sampling sites in Leschenault Estuary and each row was left for 24 h before being retrieved and emptied. On the second night, a row of pots was placed randomly in the fourth site in Leschenault Estuary and in each of the two sites in Koombana Bay. These were also retrieved and emptied after 24 h. The crab pots were linked together in groups of four in a single line so that a single flag could be used to denote their location and thus reduce the chances of that location being spotted by poachers. Catches by pots are expressed as number of crabs caught per pot per day.

The mouth of the otter trawl net was 2.6 m wide, 0.5 m high and 5 m deep. The warp and bridle lengths were 50 and 13 m, respectively. The wings consisted of 51 mm mesh, while the bunt was made of 25 mm mesh. The net was towed by a boat for a distance of *ca* 50 m at a speed of *ca* 3-4 km h^{-1}, during which time the trawl covered an area of *ca* 650 m^2. On each sampling occasion, trawling was carried out between 0800 and 1600 h in each of the three otter trawl sampling sites in both Leschenault Estuary and Koombana Bay. As with the seine net data, the catches of crabs obtained by otter trawl are expressed as a density *i.e.* number of crabs per 100 m^2.

Prior to sampling, water temperature and salinity were measured near the bottom of the water column at each seine net site in nearshore, shallow waters and at both the top and bottom of the water column at the crab pot and otter trawl sampling sites in offshore, deeper waters. The relative strength of wave (surf) action was also recorded in Koombana Bay.

Measurements

The carapace width (CW) of each crab, *i.e.* the distance between the tips of the two lateral spines of the carapace, was measured to the nearest 1 mm. The wet weight of each crab was recorded to the nearest 0.1 g.

The fact that the abdomen is far more oval in females than males, when CW is > 30 mm, was used to sex the larger crabs. Since such differences are not well defined in crabs with CW < 30 mm, the pleopods of these smaller crabs (whose characteristics differ between females and males) were dissected out and examined under a dissecting microscope. The sex of these smaller crabs was then distinguished on the basis that the male crab has two pairs of uniramous pleopods whereas the female crab has four pairs of biramous pleopods (Warner 1977). A record was made of whether female crabs were ovigerous (Smith 1982). The fact that for female *P. pelagicus,* the abdomen of the juveniles is triangular whereas that of the adults is almost circular and free of the ventral shell, was used to determine whether or not females had undergone a pubertal moult and had thus either copulated or had not copulated previously (Van Engel 1958; Ingles & Braum 1989). In each month between July 1997 and June 1998, the wet weights of the ovaries of a random sub-sample of crabs from both Leschenault Estuary and Koombana Bay that had undergone a pubertal moult were weighed to the nearest 0.01 g. The gonad weight of each female crab, that had undergone a pubertal moult, was then expressed as a percentage of its total wet body weight to determine the gonadosomatic index (GSI). The GSI was not determined for ovigerous females, *i.e.* crabs that had extruded their eggs, and the GSIs have not been provided for male crabs since they were always very low and showed a far less pronounced seasonal trend than that of female crabs.

Since female crabs that have undergone a pubertal moult and thus typically have mated will not commence growing again until after egg extrusion, which can take place within about two weeks (Ingles & Braum 1989), the carapace width at which 50% of crabs undergo a pubertal moult (CW_{50}) will also essentially correspond to the CW_{50} at first maturity. The size at which 50% of the female crabs reach maturity (CW_{50}) was thus determined from data obtained for a wide size range of female crabs in which each crab had been recorded as either having not undergone or having undergone a pubertal moult, and thus had either not reached the size or had reached the size at which copulation occurs, respectively. A logistic function was fitted to the percentage of those female crabs which, in each 5 mm carapace width interval, had undergone a pubertal moult, using a non-linear technique (Saila *et al.* 1988), employing a non-linear sub-routine in SPSS (Anon 1988). The logistic equation was $PCW = [1 + e^{(a + bCW)}] -1$, where PCW is the proportion of crabs that have undergone a pubertal moult at carapace width interval CW, and a and b are constants. The CW_{50} was derived from the equation $CW_{50} = - a/b$.

Although male crabs do not undergo a morphologically conspicuous pubertal moult, the pattern of growth of their largest chela does change markedly during that moult. This could therefore be used to estimate the size at which male crabs undergo such a moult and have thus attained the size at which they first reach maturity (Reeby *et al.* 1990; Somerton & Donaldson 1996). Male crabs were thus first separated into three categories, namely (1) juveniles that were small (*i.e.* CW < 60 mm) and thus below the minimum size at which maturity is usually reached in other populations of *P. pelagicus,* (2) adults that were large, CW > 120 mm, and were thus of a size at which maturity would be expected to have been attained, and (3) juveniles or adults in which the carapace widths lay between 60 and 120 mm. The choice of the above three categories of carapace widths was based on data recorded by Meagher (1971), Ingles & Braum (1989) and Reeby *et al.* (1990) for the size of juveniles and adults in other populations of *P. pelagicus*. The lengths of the dorsal surface of the propodus of the largest chela of crabs belonging to the first and second of these categories of crabs were then plotted against their carapace widths. Regression lines were fitted by the least sum of squares method to these two data sets, assuming $L = a + bCW$, where L is the length of the chela propodus, CW is the carapace width and a and b are constants. The two regression lines derived for the relationship between propodus length and carapace width of the (small) juvenile and (large) mature crabs, were then fitted iteratively but with incorporation of the corresponding data for the medium size category (CWs of 60-120 mm), until the two lines which had produced the lowest residual sum of squares were found. The point at which the lines now inter-

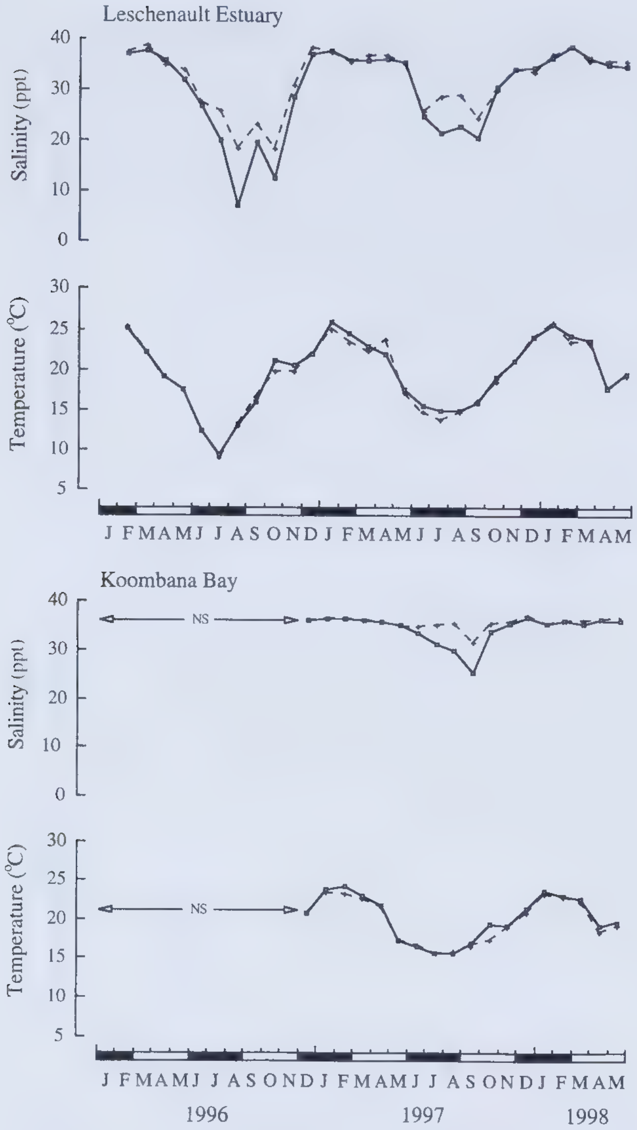

Figure 2. Mean monthly salinities and water temperatures at the bottom and top of the water column in Leschenault Estuary and Koombana Bay. NS, not sampled. ——■—— Surface; – – ▾ – Bottom.

sect was then assumed to provide a good approximation of the carapace width at which there is a pronounced change in the pattern of growth of the largest chela, a feature which is, as mentioned previously, known to be associated in males with the pubertal moult (Reeby *et al.* 1990; Somerton & Donaldson 1996). The next step involved determining whether the point for the relationship between the length of the chela propodus and the carapace width of each crab was closer to the regression line relating these two variables in "juvenile" crabs or in "adult" crabs, as defined above. Each crab was then recorded as either immature or mature, *i.e.* had undergone a pubertal moult. The logistic curve was then fitted to the percentage contributions of mature crabs in each 5 mm carapace width interval.

Diet

Stomachs were removed from sub-samples of 20-30 intermoult (hard shelled) crabs collected by seine netting and otter trawling in each season in Leschenault Estuary. These crabs were selected so that they covered the entire size range caught on each sampling occasion. The carapace width of each crab was measured. The fullness of the stomach of each crab was recorded, using a scale of 0 (empty) to 10 (full). Each dietary item was identified to the lowest possible taxon under a dissecting microscope and then allocated to one of 13 broader taxonomic categories, which are subsequently referred to as dietary categories. The volumes of each dietary category, and also of ingested sediment, were expressed using the points method (Hynes 1950; Hyslop 1980), which takes into account the overall stomach fullness. Volumetric data provide a good representation of the relative importance of each dietary category, especially in animals such as crabs, which masticate their food and thereby make it difficult to identify the number of individuals belonging to certain prey species (Hyslop 1980). The relative contributions of each dietary category and sediment to the volume in the stomach of each crab (%V) were calculated. The mean contributions of each dietary category to the total volume of the dietary contents were then calculated for crabs with carapace widths ≤ 75 and > 75 mm (CW of 75 mm approximates the mid-point of the size range of *P. pelagicus* in Leschenault Estuary).

Commercial catch

Data on the monthly catches of crabs obtained by commercial fishers using drop nets, and the corresponding data for effort, were extracted from the Fisheries Western Australia Catch and Effort Statistics (CAES). The data covers financial years, *i.e.* July to June, which is appropriate since each year then encompasses the mid spring to autumn period, when crabs are known to be most abundant in estuaries on the lower west coast of Western Australia (*e.g.* Meagher 1971; Potter *et al.* 1983).

Results

Salinity and water temperature

The following account of the trends exhibited by salinity in Leschenault Estuary initially focuses on those occurring at the bottom of the water column in offshore, deeper waters (Fig 2). This is followed by a description of the way in which the salinities at the top of the water column in those waters are modified as a result of the influence of heavy freshwater discharge in winter and how this results in the formation of pronounced haloclines. Attention is drawn to the fact that, in each month, the salinity in shallow, nearshore waters is essentially the same as that recorded at the top of the water column in offshore, deeper waters (Fig 2).

The mean monthly salinities at the bottom of the water column in offshore, deeper waters, *i.e.* 1.5-2.5 m, of Leschenault Estuary in February to April of 1996 were *ca* 35 ppt (Fig 2). They then fell sequentially in subsequent months to a minimum of 18.2 ppt in August, before rising to 23.2 ppt in September and then falling back temporarily to 18.2 ppt in October, due to an overflowing of the Wellington dam on the Collie River and thus to an increase in freshwater discharge into the estuary. They then rose progressively to *ca* 35 ppt in December 1996 and remained close to that level until May 1997, after which they declined to 24-30 ppt in

June to September. Mean monthly salinities then rose progressively to 35 ppt in December 1997 and remained at or just above this level through to May 1998 (Fig 2).

Mean monthly salinities at the surface of the water column in offshore, deeper waters of the estuary followed the same seasonal trends as those exhibited by bottom salinities (Fig 2). However, salinities at the surface declined to appreciably lower levels than those at the bottom of the water column in July to October of 1996 and in July to September of 1997. This reflects the fact that a substantial amount of the increase that occurs in the input of freshwater discharge from the Collie and Preston rivers into Leschenault Estuary in winter, following the onset of seasonal rains, flows out at the surface of the estuary and thereby produces a conspicuous halocline in those months. The maximum difference between surface and bottom salinities was the 11.1 ppt recorded in August 1996 (Fig 2).

Mean monthly water temperatures at the bottom of the water column in offshore, deeper waters of Leschenault Estuary declined sequentially from 25.4 °C in February 1996 to a minimum of 8.9 °C in July and then rose to 25.0 °C in January 1997 (Fig 2). They subsequently declined gradually to 23.7 °C in April and then more rapidly to *ca* 14.5 °C in July, before rising progressively over the ensuing six months to reach a peak of 26.1 °C in January 1998 and then declining to between 17.9 and 19.3 °C in April and May. In each month, the mean water temperatures at the surface of the water column in offshore, deeper waters of Leschenault Estuary were the same or similar to those at the bottom of the water column (Fig 2). Thus, a marked thermocline was never formed in the estuary. In each month, the mean water temperature in nearshore, shallow waters was always very similar to that recorded at the surface in offshore, deeper waters.

In Koombana Bay, the mean monthly salinities at the bottom of the water column remained at *ca* 35ppt in each month between December 1996 and May 1998, except in September 1997 when they declined to 31.6 ppt (Fig 2). Mean monthly salinities in the surface of the offshore, deeper waters of Koombana Bay remained at *ca* 35 ppt between December 1996 and May 1997, before declining sequentially to a minimum of 25.4 ppt in September, which was appreciably lower than the mean salinity at the bottom of the water column in that month. This decline in salinity was due to a continuous heavy discharge of fresh water from the Collie and Preston rivers into the lower end of Leschenault Estuary and then out through the channel into Koombana Bay. This very substantial input of freshwater into Koombana Bay accounts for the development of a pronounced halocline in this embayment in July to September 1997 (Fig 2).

Mean monthly temperatures at the bottom of the water column in offshore, deeper waters of Koombana Bay declined from 23.4 °C in January 1997 to a minimum of *ca* 16 °C in July and August 1997, before rising to 17.3 °C in October and then to a peak of 23.1 °C in January 1998 (Fig 2). In virtually all months, the mean temperature at the surface of offshore, deeper waters was usually the same or very similar to that at the bottom of the water column. However, a slight thermocline was recorded in October 1997, when the mean surface water temperature was 2 °C higher than that at the bottom of the water column (Fig 2).

As was the case in Leschenault Estuary, the mean salinity and water temperature in nearshore, shallows of Koombana Bay in any month were very similar to those at the top of the water column in offshore, deeper waters in the same month.

Monthly density and catch rates

In each month, the densities of blue swimmer crabs at the three sites in nearshore, shallow waters of the middle region of Leschenault Estuary were almost invariably not significantly different from those at the three sites in corresponding waters of the lower region of this estuary. Thus,

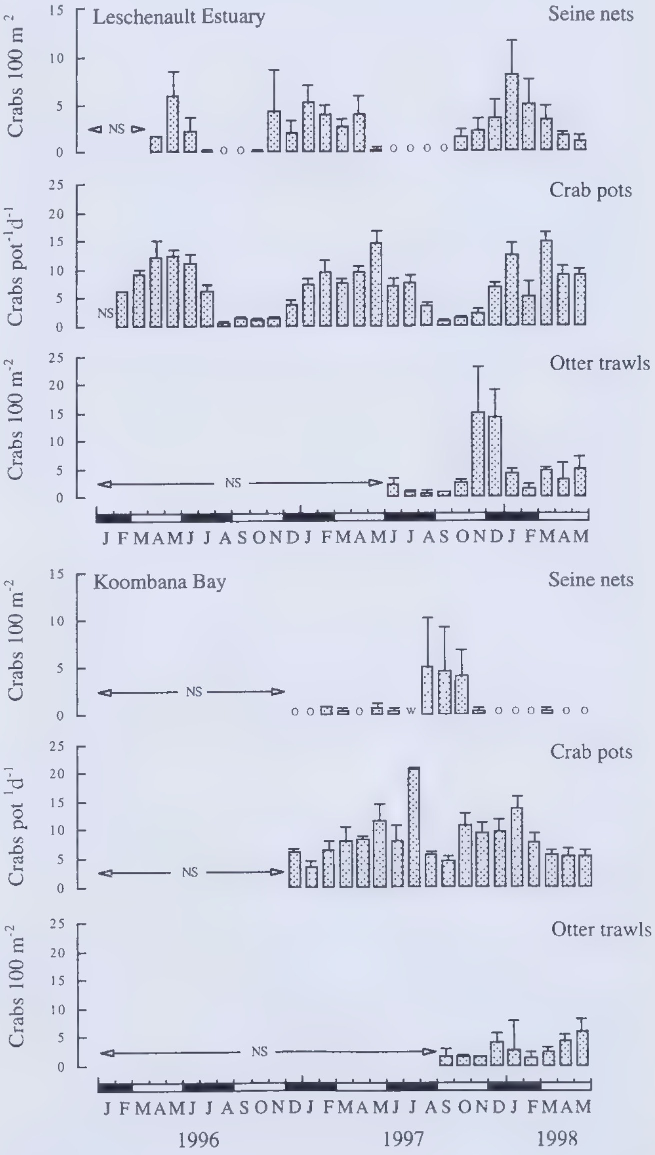

Figure 3. Mean +1 se for densities or catch rates of *Portunus pelagicus* in Leschenault Estuary and Koombana Bay, based on data derived from samples collected by seine nets in nearshore, shallow waters and by crab pots and otter trawls in offshore, deeper waters. The black rectangles on the X axis refer to summer and winter months and the open rectangles to autumn and spring months. NS, not sampled; W, wave action too strong for sampling; 0, zero catch.

the densities of crabs at each of those six seine net sampling sites in each month have been pooled. The mean monthly density of crabs in the six nearshore, shallow sites of the Leschenault Estuary declined from 5.8 crabs 100 m^{-2} in May 1996 to 0 in August and September, before rising to 4.3 crabs 100 m^{-2} in November and remaining at between 2.0 and 5.3 crabs 100 m^{-2} until May 1997, when it declined to 0.3 crabs 100 m^{-2} (Fig 3). No crabs were caught at any of the six seine net sampling sites in the estuary between June and September 1997. However, crabs were caught again at these sites in October, the catches in that month corresponding to a mean density of 1.4 crabs 100 m^{-2}. Mean monthly densities increased to 2.3 crabs 100 m^{-2} in November and then to a maximum of 7.9 crabs 100 m^{-2} in January 1998, after which they declined progressively to 1.0 crab 100 m^{-2} in May (Fig 3).

The size distributions of female crabs caught in pots with 12 mm mesh during 1996 were essentially the same as those in pots with 76 mm mesh, and this was also the case with male crabs (Fig 4). However, in the case of the catches obtained in both the 12 and 76 mm mesh pots, the proportions of crabs with a CW > 130 mm were greater for females than males, whereas the reverse pertained with crabs with a CW < 120 mm. This point is reflected by differences in the mean values for the carapace widths. Thus, the mean carapace width of female crabs caught in 12 and 76 mm mesh pots *i.e.* 124.2 and 124.9 mm respectively, were each significantly greater ($P < 0.05$) than those of male crabs caught in pots with corresponding meshes, *i.e.* 119.4 and 118.9 mm respectively. Since there was no significant difference between the mean carapace width of female crabs caught in pots with 12 and 76 mm meshes and the same was also true for male crabs, the catches of each sex in pots with both mesh sizes have been pooled (Fig 3).

The mean monthly catch of crabs pot^{-1} d^{-1} in offshore, deeper waters of Leschenault Estuary in 1996 rose from 6.2 in February to 12.5 in May, and then fell after July to < 1.3 between August and November (Fig 3). Catch rates, using the same units, began to rise in December and subsequently peaked at 14.5 in May 1997, before declining to their minima of 0.8 in September, one month later than in the previous year. Mean catch rates subsequently remained below 2.0 crabs pot^{-1} d^{-1} in October and November, but then remained at between 5.2 and 14.9 crabs pot^{-1} d^{-1} between December 1997 and May 1998 (Fig 3).

The mean monthly densities of crabs in offshore, deeper waters, based on data obtained from otter trawl samples collected in similar regions of the Leschenault Estuary as those in which the traps were laid, declined from 2.1 crabs 100 m^{-2} in June 1997 to less than 0.6 crabs 100 m^{-2} in August and remained below 0.9 crabs 100 m^{-2} in September, before rising sharply to *ca* 15 crabs 100 m^{-2} in both November and December (Fig 3). Mean monthly densities in January to May 1998 lay between 1.5 and 5 crabs 100 m^{-2}.

The mean monthly densities of crabs in the shallows of Koombana Bay, based on data derived from samples collected by seine netting in the three widely-distributed nearshore, shallow sites in this embayment, were either zero or less than 0.8 crabs 100 m^{-2} in all months except August, September and October 1997, when they lay between 4.0 and 5.1 crabs 100 m^{-2} (Fig 3).

The mean monthly catch rate of crabs by pots in offshore, deeper waters of Koombana Bay showed no consistent

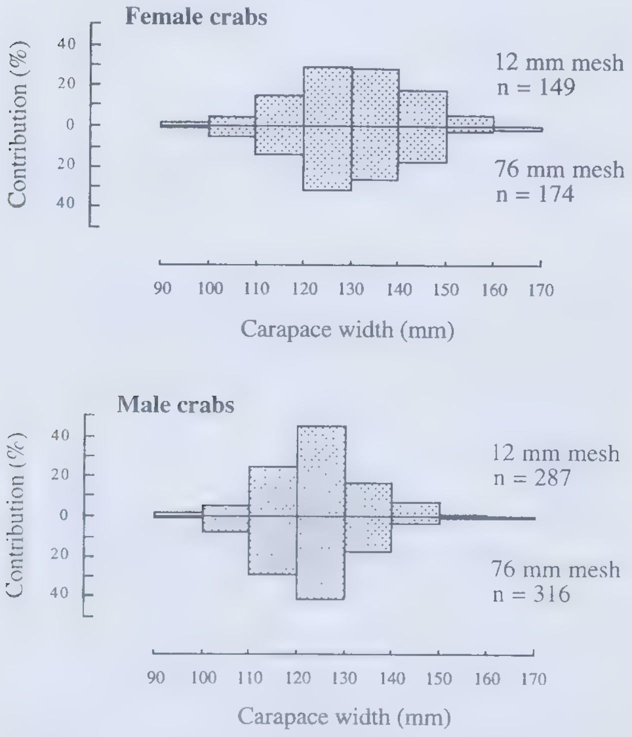

Figure 4. Carapace-width histograms for female and male *Portunus pelagicus* caught by crab pots with 12 and 76 mm meshes between February 1996 and January 1997. n is the number of crabs measured.

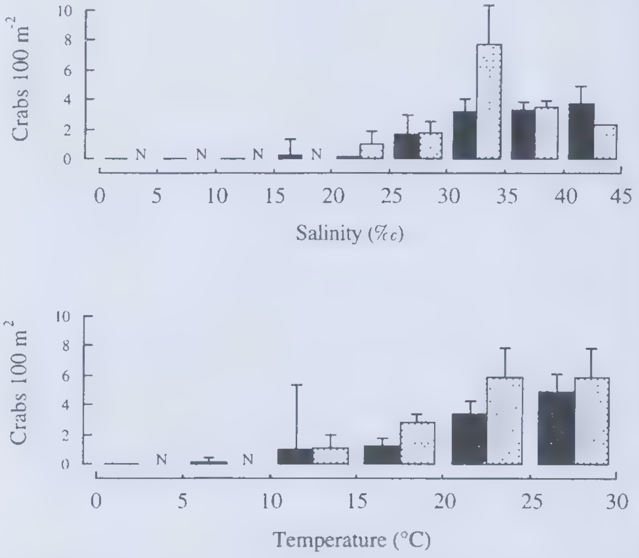

Figure 5. Mean +1 se for densities of *Portunus pelagicus* in different salinity and water temperature intervals in nearshore, shallow and offshore, deeper waters of the Leschenault Estuary, based on data collected using seine nets between April 1996 and May 1998 and otter trawls between June 1997 and May 1998, respectively. Values for salinities and temperatures at the bottom of the water column were used in the case of deeper waters. N indicates that salinities and temperatures were not recorded in deeper, offshore waters during sampling by otter trawl. ■ Nearshore, shallow waters; ▨ Offshore, deeper waters.

seasonal trends during the study (Fig 3). The overall mean catch rate throughout the sampling period was 8.3 crabs pot^{-1} d^{-1}, with the highest mean monthly catch rate in this period being the 20.7 crabs pot^{-1} d^{-1} recorded in July 1997 (Fig 3). Otter trawling in Koombana Bay between September 1997 and May 1998 yielded catches that corresponded to mean monthly densities of 1.3 to 5.1 crabs 100 m^{-2} (Fig 3).

The mean densities of *P. pelagicus* in nearshore, shallow waters of Leschenault Estuary, based on samples collected by seine net, were similar in each of the three 5 ppt salinity intervals between 30 and 45 ppt, with values for these intervals ranging only from 3.2 to 3.7 crabs 100 m^{-2} (Fig 5). Few crabs were caught in the shallows when salinities were < 20 ppt. The mean densities of crabs in offshore and slightly deeper waters, based on samples collected by otter trawl, lay between 1.1 and 7.7 crabs 100 m^{-2} in each 5 ppt salinity interval between 20 and 45 ppt and were greatest in salinities of 30.0-34.9 ppt and least in salinities of 20.0-24.9 ppt.

The mean densities of crabs in nearshore, shallow waters of Leschenault Estuary ranged downwards from 4.9 crabs 100 m^{-2} in water temperatures of 25-29.9 °C to 3.4 crabs 100 m^{-2} in 20.0-24.9 °C and 1.0 crabs 100 m^{-2} in 10.0-14.9 °C (Fig 5). A similar trend was observed in offshore, deeper waters, where the mean densities declined from *ca* 5.9 crabs 100 m^{-2} in 20.0-29.9 °C to 1.1 crabs 100 m^{-2} in 10.0-14.9 °C. Virtually no crabs were caught in the estuary when water temperatures fell below 10 °C.

Size and growth

Since the carapace width of crabs caught in Leschenault Estuary by pots with both 12 and 76 mm mesh were > 90 mm in the 12 months between February 1996 and January 1997 (Fig 4), and yet many crabs were present in the estuary below this size at certain times of the year, there was a high level of selectivity for large crabs using pots. The size data for crabs in pots have thus not been included in the monthly size-frequency histograms shown in Figs 6 and 7. Since the monthly trends exhibited by the size-frequency data for *P. pelagicus* in seine net samples collected in Leschenault Estuary were the same in each year and the same was true for Koombana Bay, the carapace width data given in Figs 6 and 7 for crabs in both water bodies have utilised pooled size data obtained from seine netting in each of the corresponding months of the different years.

Samples of female crabs collected in Leschenault Estuary in June contained a small group of small crabs with carapace widths between 30 and 90 mm and a small group of larger crabs with carapace widths between 100 and 160 mm (Fig 6). In July to September, the cohort of larger crabs was no longer present and the smaller crabs were present in only very low numbers. The cohort, which corresponded to the smaller crabs caught in June, started to increase in numbers in October and was still well represented in May, by which time its size range corresponded to that of the small group of larger crabs caught in June. The modal carapace width class of this cohort had increased from 60-69 mm in November to 70-79 mm in December and 90-99 mm in January to 100-109 mm in March and 110-119 mm in May (Fig 6). Small numbers of a new cohort of small crabs, with carapace widths of 30 to 79 mm, were present in February to May. These corresponded to the cohort of small crabs found in June. The trends exhibited by the monthly carapace-width frequency histograms for male crabs were essentially the same as those just described for female crabs (Fig 6).

The above trends demonstrate that small crabs, representing the 0+ age class, are recruited into Leschenault Estuary in small numbers in late summer and autumn. The numbers of this cohort in the estuary then decline in winter and early spring, before starting to rise markedly in mid to late spring as the water temperatures start increasing markedly. This cohort was represented by large numbers in December to February, in which months its members were, on the basis of a late spring/summer spawning period (see later), now *ca* 1 year old. The corresponding cohort, now representing 1+ crabs, was relatively abundant until late autumn, but then declined in numbers in June and had essentially disappeared from the estuary in the ensuing winter and early spring months.

The size distributions of both female and male crabs caught collectively by seine net and otter trawl in Koombana Bay were similar in each month between August and December, with the vast majority of both sexes having a CW > 80 mm (Fig 7). The carapace widths of the corresponding cohort increased slightly in the ensuing months, and more particularly in the case of male crabs. The new 0+ cohort, represented by crabs with carapace widths of 20 to *ca* 90 mm, first appeared in low numbers in February and in more substantial numbers in April and May (Fig 7).

The carapace widths of all female and male crabs caught by crab pots in each month of the year in the Leschenault Estuary and Koombana Bay were almost invariably > 90 mm (Fig 8). Indeed, the modal carapace width was usually between 100 and 130 mm. The virtual absence in pots of crabs with a CW < 90 mm may reflect avoidance of the bait in pots by smaller crabs as a result of the more aggressive behaviour of large crabs (Warner 1977) and/or a greater preference of larger crabs for fish (see later), which was used as bait. The modal carapace widths did not thus show a progression of the type that was exhibited by crabs caught in Leschenault Estuary using seine nets and otter trawls (*cf* Figs 6, 8). It is also noteworthy that, while all of the crabs caught in seine nets and otter trawls between the middle of winter and early spring had a carapace width < 120 mm (Fig 6), a few crabs with carapace widths > 120 mm were caught in pots during this period (Fig 8). This indicates that a few 1+ crabs remain in the estuary during this period.

Sex ratio

The overall sex ratios of crabs that had a CW < 90 mm and were caught by otter trawl in Leschenault Estuary and Koombana Bay in the different months were often close to parity, particularly in Leschenault Estuary (Fig 9). A Chi-squared test showed that there was no significant overall deviation from a 1:1 ratio of females to males in either locality. However, amongst crabs with a CW > 90 mm in the samples collected by otter trawl, the ratio of females to males was significantly less than parity in Leschenault Estuary (1:1.8), whereas the reverse was true for Koombana Bay

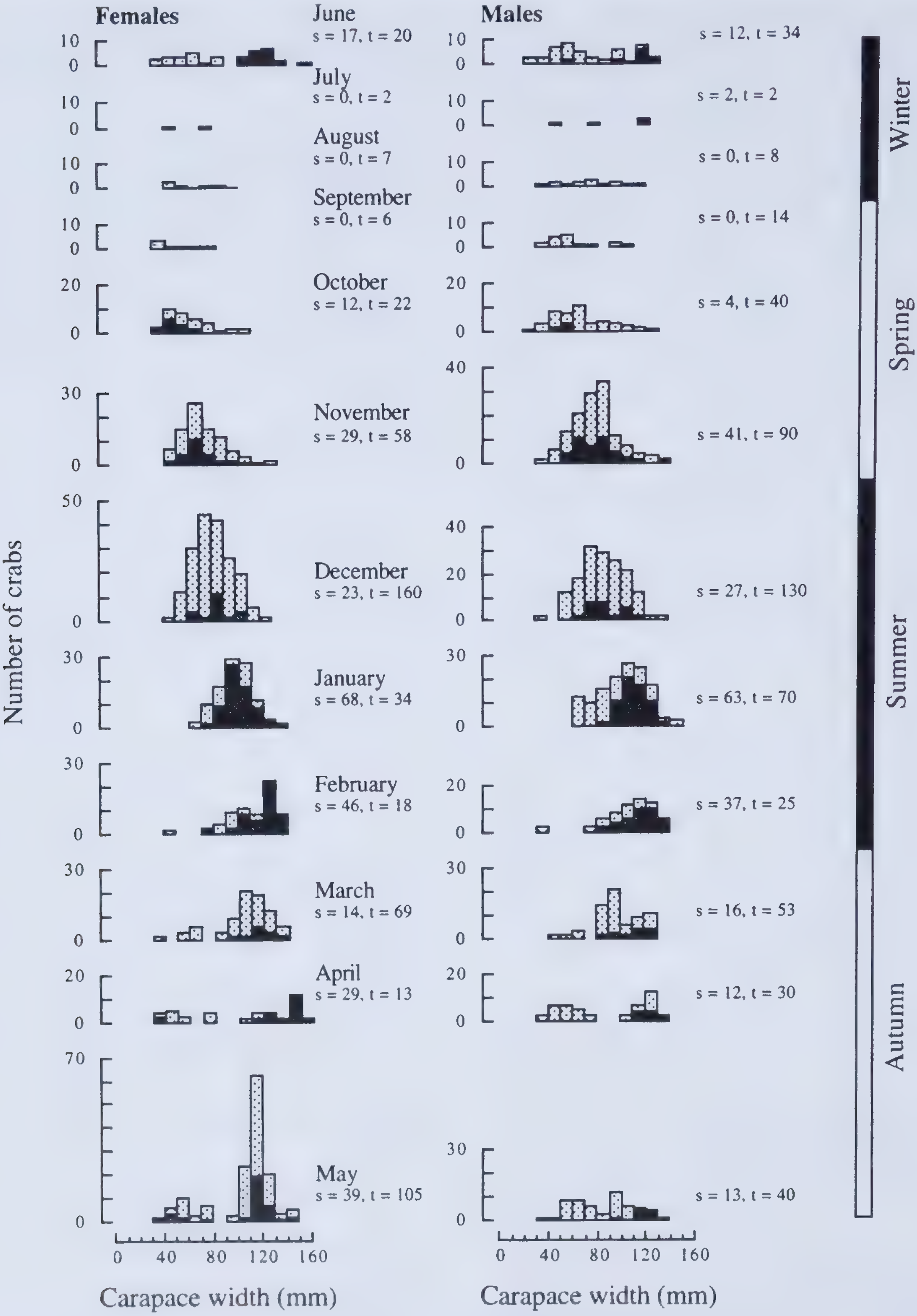

Figure 6. Monthly frequency histograms for the carapace widths of female and male *Portunus pelagicus* in Leschenault Estuary, based on data derived from samples collected by seine net in nearshore, shallow waters between April 1996 and May 1998 and by otter trawl in offshore, deeper waters between June 1997 and May 1998. The data obtained by both methods in each month have been adjusted to correspond to a total area sampled of 2000 m^{-2}, which is similar to the area covered during the three otter trawls carried out monthly in any one year and by seine netting in the corresponding months over three years. Number of crabs caught by seines and trawls are denoted by s and t, respectively.

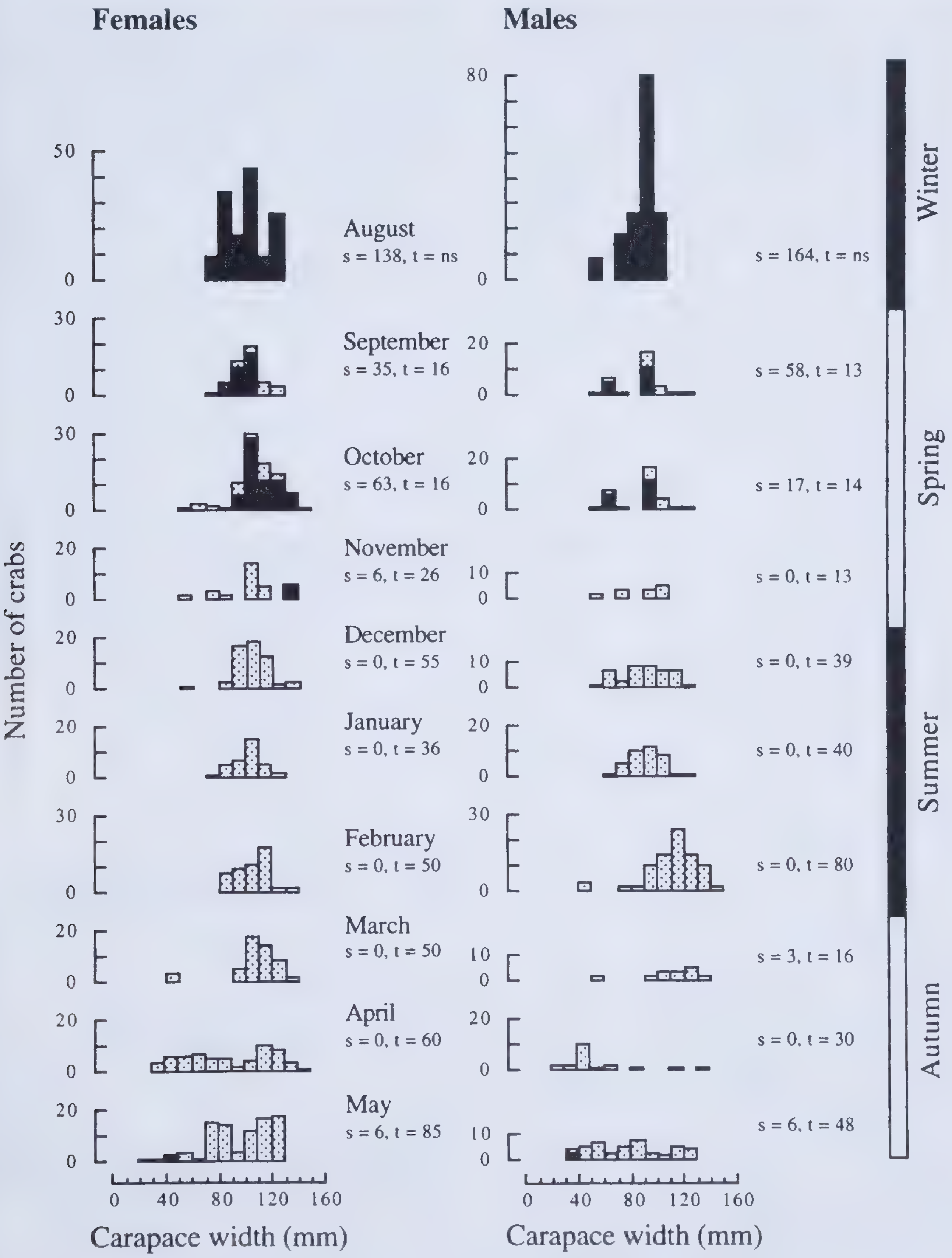

Figure 7. Monthly frequency histograms for the carapace widths of female and male *Portunus pelagicus* in Koombana Bay, using data derived from samples collected by seine nets in nearshore, shallow waters between December 1996 and March 1997 and by otter trawls in offshore, deeper waters between September 1997 and March 1998. The data obtained by both methods in each month have been adjusted to correspond to a total area sampled of 2000 m^2, which is similar to the area covered during the three otter trawls carried out monthly in any one year and by seine netting in the corresponding months over three years. Number of crabs caught by seines and trawls are denoted by s and t, respectively.

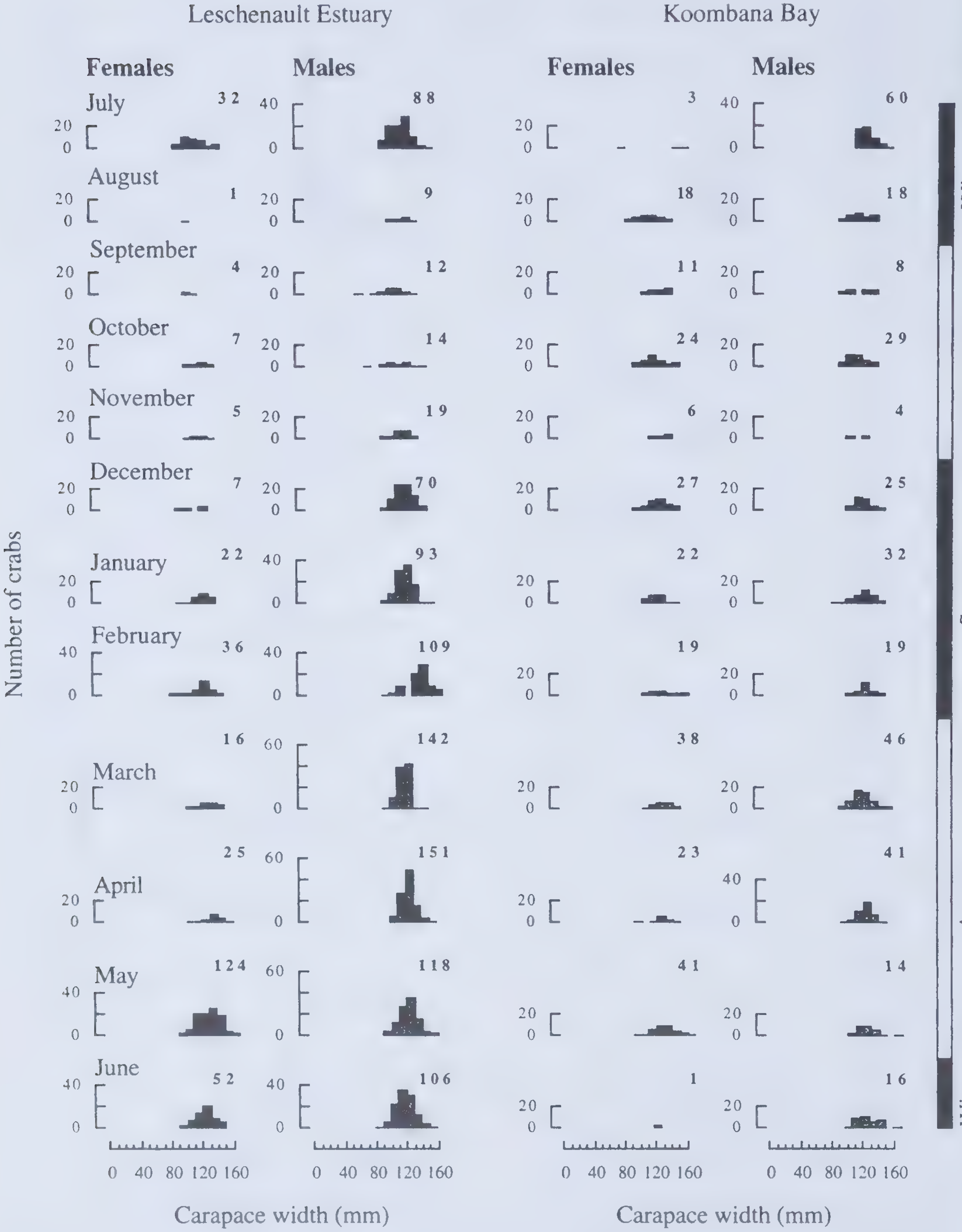

Figure 8. Monthly frequency histograms for the carapace widths of *Portunus pelagicus* caught in crab pots in Leschenault Estuary between February 1996 and May 1998 and in Koombana Bay between 1996 and May 1997. Data for the corresponding months of the year have been adjusted so that they correspond to a monthly mean. Sample size is given for each monthly catch of female and male crabs.

(1:0.5). Although the ratio of females to males in pot catches was likewise greater in Leschenault Estuary, this difference was even more pronounced, with the overall sex ratio of females to males being 1:3.8. The sex ratio also differed significantly from parity in the case of crab pot catches obtained from Koombana Bay, but in this case the difference between the contributions of the two sexes was not as extreme, with the overall ratio of females to males being 1 to 1.7. However, in both Leschenault Estuary and Koombana Bay, the proportion of female crabs was less in the samples obtained by crab pots than in those that were caught by otter trawls and likewise had a CW > 90 mm. This implies that crab pots have a greater tendency to catch male than female crabs, which may be related to the greater levels of activity exhibited by male crabs (Sumpton & Smith 1990).

Reproductive biology

The smallest female *P. pelagicus* that had undergone a pubertal moult in Leschenault Estuary and Koombana Bay and could thus be characterised as having attained the size at which maturity occurs, had a carapace width of 94 mm. Maturity was attained by *ca* 75% of female crabs with carapace widths of 100-105 mm and by all of those with carapace widths of 125-130 mm (Fig 10). The logistic curve fitted to the data for the percentage numbers of female crabs that had undergone a pubertal moult in sequential 5 mm carapace width intervals yielded a value of 97 mm for the carapace width at which 50% of female crabs first become mature (Fig 10). The corresponding CW_{50} for male crabs was 84 mm (Fig 10).

The mean monthly GSIs of female crabs in Koombana Bay in 1997, utilising data for individuals that had undergone a pubertal moult, rose progressively from 1.2 in July to a maximum of 4.6 in October, before declining to 1.7 in December (Fig 11). They subsequently fell to their minima of *ca* 0.2 in February and March of 1998, but then increased to 1.5 in May, a value similar to that recorded in July 1997. Although the trends exhibited by the mean monthly GSIs of female crabs were similar in Leschenault Estuary to those exhibited in Koombana Bay, the maximum values were far lower, *i.e.* 1.9 *vs* 4.6 (Fig 11).

Between July 1997 and May 1998, ovigerous females were found in Koombana Bay in each month between October and January and in May and in the Leschenault Estuary in each month between November and May except for February and April (Fig 11). However, the majority of ovigerous females was caught in November to January in Koombana

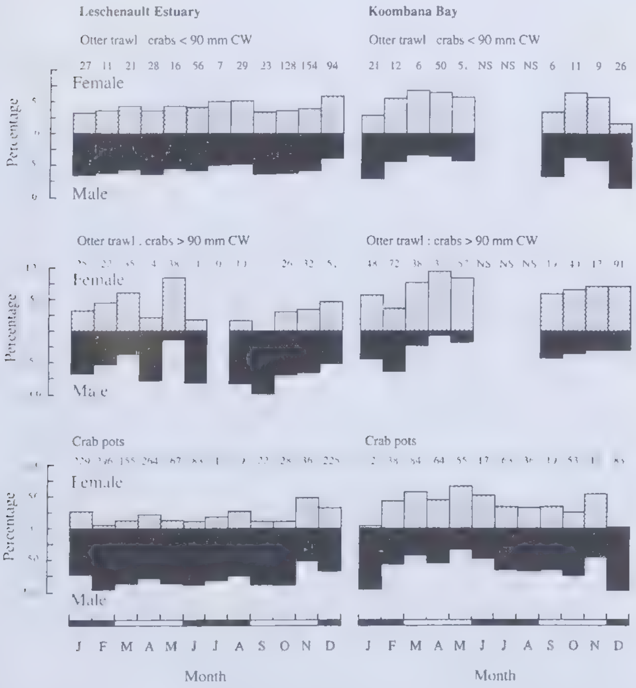

Figure 9. Percentage number of female and male *Portunus pelagicus* in samples collected by otter trawls and crab pots, respectively. Monthly sample sizes are given above each histogram. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

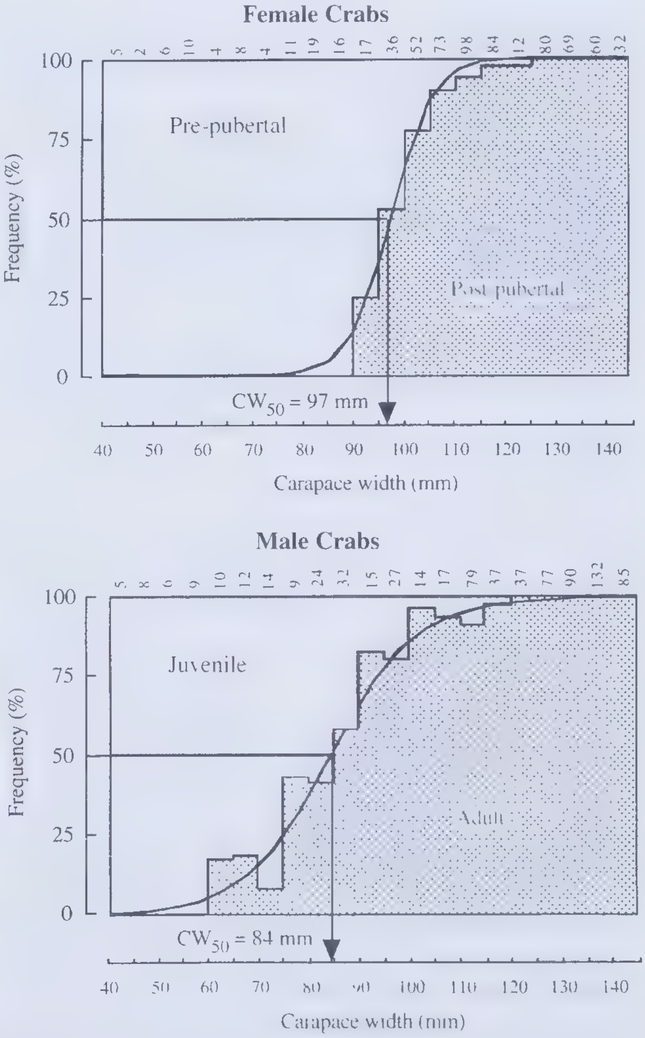

Figure 10. Top: Percentage of those females in each sequential 5 mm carapace width interval which had not undergone a pubertal moult and would thus not have mated and for those which had undergone a pubertal moult and were therefore of mature size. The logistic curve was fitted to the percentage of crabs that had undergone a pubertal moult in order to determine the CW_{50} at first maturity. Bottom: For males, the logistic curve was fitted to the carapace widths of those crabs which, from the relationships between the lengths of the propodus of the largest chela and the carapace widths, were capable of mating and were thus adults of mature size (see text for full details of methodology). Arrows denote CW_{50} for size at maturity of female and male crabs.

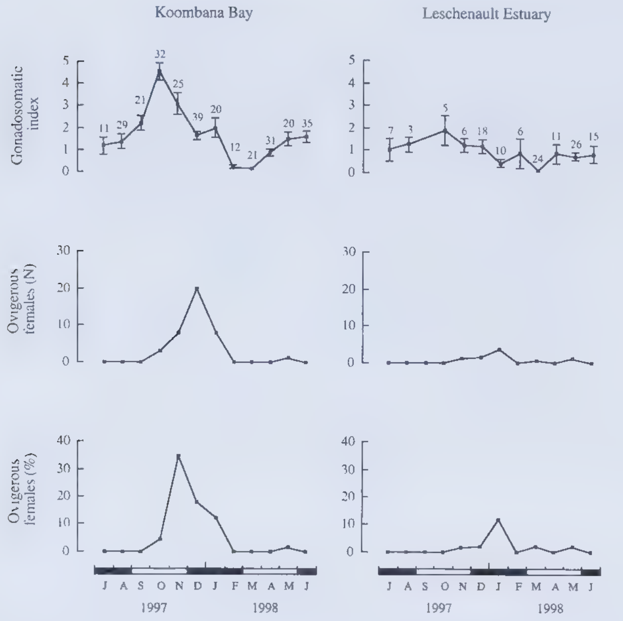

Figure 11. Monthly values for the mean gonadosomatic index ±1 se of female crabs, which had undergone a pubertal moult, the number of ovigerous female crabs and the prevalence (%) of ovigerous crabs amongst female crabs with a CW > 97 mm, the CW_{50} at which female crabs first reach maturity. The numbers and prevalence of ovigerous crabs caught monthly in Koombana Bay have been adjusted so that they are based on the same effort as that employed monthly in Koombana Bay, *i.e.* the use of three seines, three otter trawls and eight crab pots in each month. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

Bay and in December and January in Leschenault Estuary. Furthermore, both the numbers and prevalence of ovigerous crabs were far greater in Koombana Bay than in Leschenault Estuary (Fig 11). This point is emphasised by the fact that the maximum monthly values for the number and prevalence of ovigerous crabs were 20.0 and 34.8% in Koombana Bay, respectively, and 4.9 and 11.9% in Leschenault Estuary, respectively. The above trends exhibited by the prevalence of ovigerous crabs parallels those recorded in the previous year, based on data derived from samples that were collected using just seine nets and crab pots (data not shown). The above data on ovigerous females provide overwhelming evidence that spawning occurs in Koombana Bay and that it takes place predominantly between the middle of spring and middle of summer.

Diet

Based on pooled samples for all size classes of intermoult *i.e.* hard shelled crabs, the assemblage of *P. pelagicus* in Leschenault Estuary feeds largely on a wide range of benthic invertebrates, such as amphipods, polychaetes, bivalve molluscs, and also on teleosts *e.g.* gobiids. However, the diets of small crabs (CW ≤ 75 mm) and large crabs (CW > 75 mm) differ. Thus, for example, the volumetric contribution made to the diet by amphipods declined markedly from 41.6% in small crabs to 13.3% in large crabs, whereas those of polychaetes and teleosts rose from 13.1 and 2.2% to 27.0 and 10.3%, respectively (Fig 12).

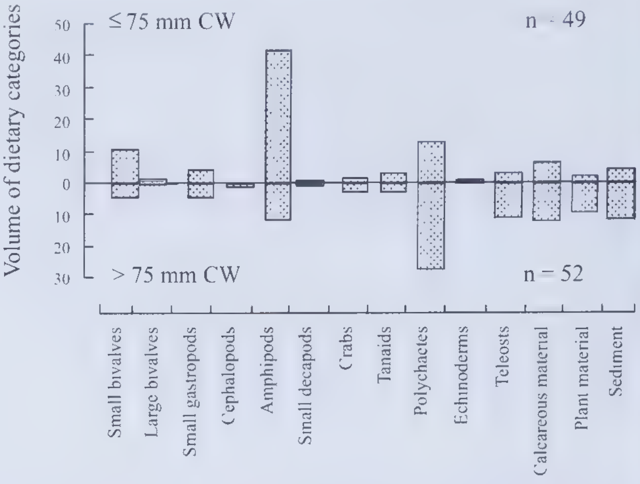

Figure 12. Frequency histograms showing the percentage contributions of the volume of different dietary categories to the total volume of the diets of two size categories (CW ≤ 75 and > 75 mm) of *Portunus pelagicus* collected in Leschenault Estuary. n is the number of samples.

Commercial fishery

The annual commercial catches of blue swimmer crabs in Leschenault Estuary between 1983/84 and 1995/96 ranged from a low of 1 027 kg in 1993/94 to a high of 7 700 kg in 1983/84 (Fig 13), with an annual mean of 4 382 ± 566.9 (se) kg. The annual commercial fishing effort for blue swimmer crabs, as measured by the total number of days spent fishing by commercial fishers for this portunid each year, remained above 130 days year^{-1} from 1983/84 to 1992/93, except in 1988/89, but then declined to < 108 days year^{-1} from 1993/94 to 1995/96 (Fig 13). The maximum number of days spent fishing in any one year was the 228 days in 1989/90. In contrast to effort, the highest catch per unit efforts (CPUEs), as reflected by kg wet weight of crabs caught per days fished, were recorded in 1994/95 and 1995/96. The minimum and maximum annual values for CPUE *i.e.* 61.0 and 312.1 kg wet weight per days fished, were recorded in 1988/89 and 1994/95 respectively.

The mean monthly commercial catches of blue swimmer crabs in Leschenault Estuary changed markedly throughout the year (Fig 14). Thus, they were very low in July to November *i.e.* < 122 kg, but then rose markedly to 532 kg in December and 1 211 kg in January, before subsequently falling sequentially to 484 kg in April, 214 kg in May and 52 kg in June. The mean monthly values for effort followed the same pattern as that exhibited by catch (Fig 14). Thus, the total number of days spent fishing for crabs remained less than four in each month between July and November, before rising to maxima of 31 in January and 26 in February, and then declining sequentially in each ensuing month to only two days in June. Although the monthly trends exhibited by CPUE were very similar to those displayed by catch and effort, the CPUE started to rise slightly earlier *i.e.* September to November, and reached a maximum one month later *i.e.* February (Fig 14).

A creel census (*per. com.* N. Sumner *et al* Fisheries WA 2000) conducted by Fisheries Western Australia demonstrates that there is a considerable recreational fishery for *P. pelagicus* in Leschenault Estuary.

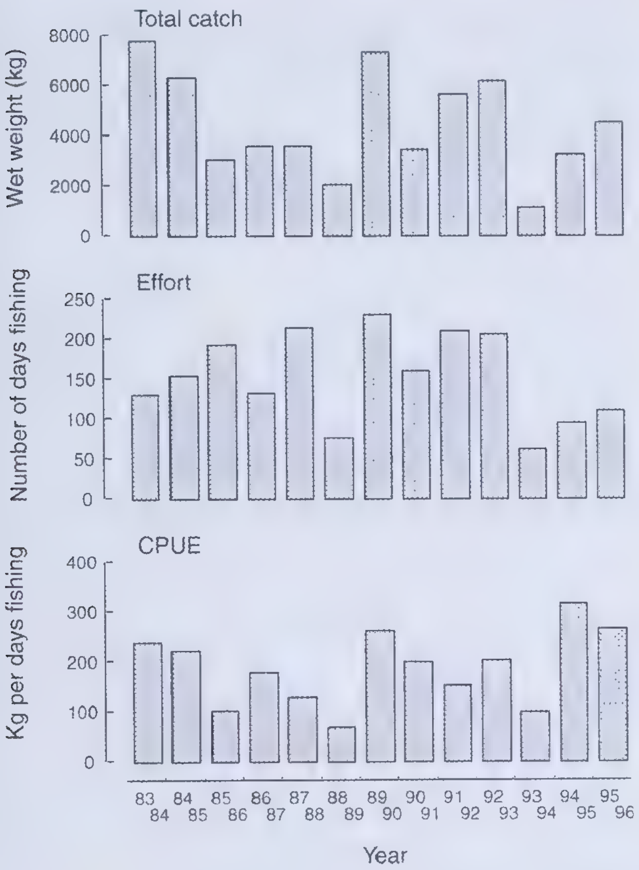

Figure 13. Annual values for total catch, effort and catch per unit effort (CPUE) for the commercial fishery for *Portunus pelagicus* in Leschenault Estuary between 1983/84 and 1995/96. Each "year" runs from 1 July to 30 June.

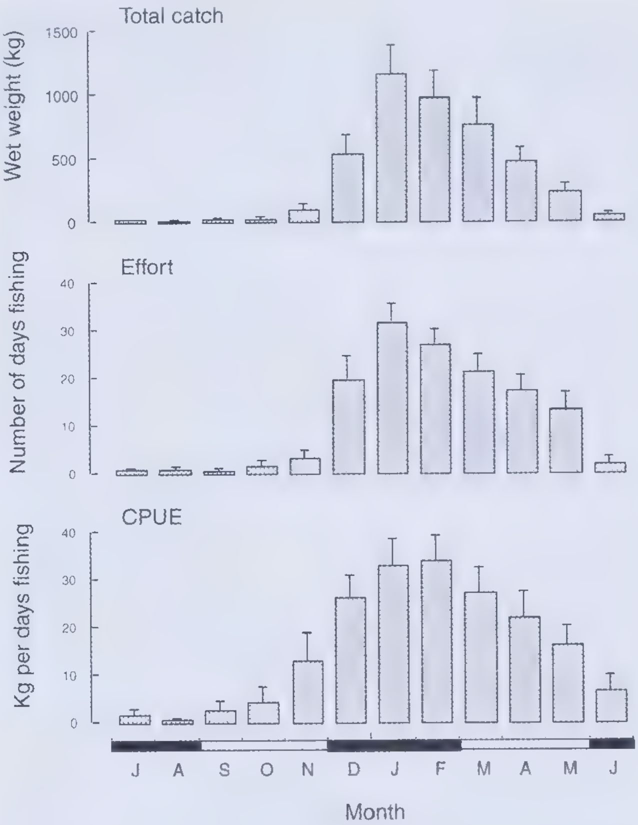

Figure 14. Mean monthly values +1 se for total catch, effort and catch per unit effort (CPUE) for the commercial fishery for *Portunus pelagicus* in Leschenault Estuary between 1983/84 and 1995/96. The black rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

Discussion

Seasonal trends

The mean monthly densities of *Portunus pelagicus* in nearshore, shallow waters of Leschenault Estuary, based on data derived from seine net sampling, were highest between mid-spring and mid-autumn and declined to very low or zero levels during winter and early spring. Although the catch rates derived from data using pots in offshore, deeper waters followed similar seasonal trends, they tended to start rising markedly a little later, *i.e.* early summer *vs* early to mid spring, and to remain at a relatively high level for longer, *i.e.* until mid winter *vs* mid- to late autumn. The tendency for the catches in pots to start increasing later can be attributed to the fact that it is not until early summer that the carapace widths of a substantial number of crabs in the estuary start to exceed 90 mm, the minimum size at which crabs are usually caught by crab pots. The maintenance of relatively high catches in pots in offshore, deeper waters for a longer period than in nearshore, shallow waters may reflect in part a tendency for crabs in autumn to move from the shallows, as salinities begin to decline markedly in those waters, out into deeper waters below the halocline where salinities remain higher. It may also be related to the characteristics of the regime we used to sample with crab pots. For example, it is likely that pots soon become "saturated" in summer, when crabs are abundant, but because they were always laid for a long period (24 hours), they were still able to approach or even reach "saturation" in mid-winter, even though fewer crabs remained in the estuary at this time. The view that increases in the number of crabs in a pot during summer would increasingly reduce the likelihood of further crabs entering that pot, and thus lead relatively soon to saturation, is consistent with the results of studies on other portunid species (see Williams & Hill 1982).

The conclusion that the tendency for the catches of crabs by pots to remain high well into winter may not reflect precisely the trends exhibited by the relative abundance of crabs in the estuary is supported by the fact that they do not parallel precisely those displayed by the mean monthly values for the CPUE for the commercial fishery, a fishery which is based on using drop nets for 25-30 minutes on eight or nine occasions during the day. Thus, in contrast to the trends exhibited by crab pot catches, the CPUE for the commercial fishery declined progressively after January and February, with the result that by June it was less than 20% of the values in those two earlier months. Yet, the possibility cannot be excluded that this decline in CPUE also partly reflects the influence of declining temperatures on the activity of crabs and thus their catchability by "passive" fishing methods such as drop netting (Hill 1980; Williams & Hill 1982). Since water temperatures are particularly low between the middle of winter and early spring, such an effect could be invoked to account in part for the particularly low catches recorded in crab pots during that period. However, it is relevant that the catches of crabs obtained by the active fishing methods of seine netting and otter trawling, which, unlike those collected in pots also include small crabs, likewise fell to very low levels in winter and early spring, but then rose sharply during late spring as salinities and water temperatures started to rise markedly. There can thus be little doubt that crab numbers in the estuary undergo a real and pronounced decline in winter, when salinities and water temperatures decline to their lowest levels.

From our data, it is evident that juvenile *P. pelagicus* start to enter Leschenault Estuary in substantial numbers during spring and that, while their abundance peaks in summer, substantial numbers of crabs are still found in this estuary until early autumn. Since the marked decline in crab numbers that subsequently occurs in the estuary during winter and early spring is accompanied by a conspicuous rise in the densities of crabs in the shallows of Koombana Bay at these times, it is assumed that at least some of the crabs which emigrate from the estuary in winter, move into nearshore, shallow waters of the above embayment. However, although the largest catch taken by pots in offshore deeper waters of Koombana Bay was recorded in winter, there was no marked tendency for the catch rates by pots in that environment to show any conspicuous seasonal trend. Thus, a substantial number of larger crabs, *i.e.* those of a size that are caught in pots, are present in offshore, deeper waters of Koombana Bay throughout the year. In this respect, our data support the conclusions of Anon (1983), rather than those of Meagher (1971) who considered that virtually all of those crabs that are in Koombana Bay at the end of winter subsequently migrate into the estuary in spring.

Our data, and also those for the Peel-Harvey Estuary (Potter *et al.* 1983), demonstrate that the densities of *P. pelagicus* are greatest in estuaries when salinities and water temperatures are high and that they are very low when these variables decline below 25 ppt and 10 °C, respectively. However, since the trends exhibited by salinities and water temperatures are highly correlated, it is dangerous to use techniques, such as stepwise multiple regressions, to attempt to disentangle which of these variables has the greatest influence on the movements of crabs into and out of the Leschenault Estuary. However, a comparison of the situation in Leschenault Estuary with that in the Peel-Harvey Estuary indicates that salinity exerts a profound influence on whether or not crabs remain within the estuary. For example, it is relevant that, although the overall trends exhibited by the density data in the Leschenault Estuary broadly parallel those recorded earlier in the Peel-Harvey Estuary (Potter *et al.* 1983), the prevalence of the 0+ age class between mid-winter and early spring was greater in samples collected from the latter system. This difference can be attributed to the fact that most of the crabs caught in the Peel-Harvey Estuary during that period were obtained from within the 5 km long entrance channel, where salinities almost invariably remained relatively high *i.e.* > 25 ppt, whereas such high salinities did not persist in Leschenault Estuary during winter. Moreover, crabs were no longer caught between mid-winter and early spring in either the saline river or more distal basin regions of the Peel-Harvey Estuary where, during that period, salinities typically decline to less than 10 ppt. This provides strong circumstantial evidence that the marked declines in salinity which occur in Leschenault Estuary during winter are likely to be the major factor initiating the emigration of crabs from this estuary at that time. However, it is also relevant that, during that period, some 0+ crabs do remain in Leschenault Estuary, whereas the vast majority of 1+ crabs leave that estuary. This suggests that 1+ crabs are even more sensitive than 0+ crabs to any marked declines in salinity.

Spawning period and location

The fact that the vast majority of the ovigerous females of *P. pelagicus* that were caught in Koombana Bay were collected between October and January provide strong evidence that this species spawns in this embayment during these months. Such a conclusion is consistent with the presence of large numbers of *P. pelagicus* zoea in plankton tows carried out by Le Provost *et al.* (1983) in Koombana Bay in mid to late November of 1982. The prevalence of ovigerous females of *P. pelagicus* is also greatest in late spring to mid-summer in Cockburn Sound (Penn 1977), a marine embayment to the north of Koombana Bay (Fig 1), and *P. pelagicus* zoea were abundant in plankton samples collected in Cockburn Sound during summer (Penn 1977). Thus, the main spawning period in Cockburn Sound is essentially the same as in Koombana Bay. Since female crabs in temperate waters remain ovigerous for about three weeks (Yatsuka 1962) and the abundance of ovigerous female crabs in Koombana Bay peaked in December, the presumptive zoea would typically be released into the water in January. Furthermore, the contrast between the abundance of crab zoea in samples collected in Koombana Bay and their absence or paucity in those obtained using the same methods in Leschenault Estuary (Meagher 1971; Anon 1983) provides strong circumstantial evidence that *P. pelagicus* typically spawns within the bay rather than the estuary.

The month when the number and prevalence of ovigerous females in Koombana Bay peaked, *i.e.* December and November respectively, was one month and two months earlier respectively, than was the case in Leschenault Estuary. The prevalence of ovigerous females in the Peel-Harvey Estuary, just to the north of the Leschenault Estuary (Fig 1), peaked in January and February (Potter *et al.* 1983), *i.e.* during a similar period as in the Leschenault Estuary. The earlier peak in ovigerous females in Koombana Bay than Leschenault Estuary can be related to the fact that large females, *i.e.* those belonging to the 1+ age class, remain in Koombana Bay during spring and early summer and are thus at a size and stage in maturity that enables them to spawn as soon as environmental conditions provide the appropriate trigger. In contrast, crabs entering the Leschenault Estuary in spring belong predominantly to the 0+ age class and are thus of a far smaller size, with the result that a substantial proportion of crabs do not start attaining a size equivalent to the CW_{50} at first maturity until December. It is also evident that, on the basis of the same measure of effort, both the number and prevalence of ovigerous females during the spring and summer were far greater in Koombana Bay than in the estuary. During the initial part of this period, this could likewise reflect in part the presence of many 1+ female crabs in Koombana Bay but not Leschenault Estuary, and thus the far greater likelihood of mating occurring. However, it is also possible that it reflects a tendency for females to leave the estuary as soon as egg extrusion has occurred and for those ovigerous females to remain for a period in Koombana Bay before releasing their fertilised eggs.

In the context of the movement of female crabs out of the estuary, it is relevant that, in otter trawl catches, the sex ratio of crabs with a CW < 90 mm was close to parity in both Leschenault Estuary and Koombana Bay, whereas with crabs with a CW > 90 mm, the proportion of females was less than males in the estuary but greater than for males in the bay. This implies that, once female crabs reach the size at which they become mature, they have a greater tendency to move out of the estuary into Koombana Bay than do males of comparable size. This conclusion is consistent with the fact that, in the crab pot catches which contained crabs exclusively with a CW > 90 mm, the ratio of females to males was also far greater in Koombana Bay than Leschenault Estuary. Indeed, the fact that, during spring and summer, the mean monthly GSIs for female crabs, which had undergone a pubertal moult, were far lower in Leschenault Estuary than in Koombana Bay suggests that some female crabs may even leave the estuary for the bay before ovarian development is very advanced. However, since several of the larger female crabs, that were caught in the estuary during late summer and autumn had undergone a pubertal moult, but did not contain full spermathecae and were not ovigerous, some female crabs do apparently return to the estuary after spawning.

Length and age at first maturity

The minimum and maximum size at which female *P. pelagicus* was first found to attain sexual maturity in Leschenault Estuary correspond to carapace widths of 94 and 122 mm, with the carapace width at which 50% of the female crabs first reach maturity being estimated as 97 mm. The corresponding CW_{50} for males was 84 mm. These values are very similar to those recorded for *P. pelagicus* in the Peel-Harvey Estuary (de Lestang & Potter, School of Biological Sciences and Biotechnology, Murdoch University, unpublished data) and in Karwar on the coast of India (Sukumaran & Neelakantan 1996b). Rather higher CW_{50}s of 106 and 96 mm at first maturity were recorded by Ingles & Braum (1989) for female and male *P. pelagicus* in the Philippines.

The CW_{50}s for female and male crabs lie well within the discrete size group that in mid summer corresponds to crabs that are approximately one year old. Indeed, since the vast majority of female crabs that were at the beginning of their second year of life had undergone a pubertal moult, most crabs probably spawn when they are one year old. This parallels the situation found with *P. pelagicus* in South Australia (Smith 1982) and Moreton Bay in Queensland (Sumpton *et al.* 1994).

Diet

The composition of the diet recorded for *P. pelagicus* in this study demonstrates that, in the Leschenault Estuary, this species feeds mainly on slow-moving or relatively sessile benthic macroinvertebrates, such as amphipods, polychaetes, and bivalve and gastropod molluscs, and to a limited extent also on slow-moving benthic teleosts such as gobies. This species can thus be regarded as a benthic carnivore, thereby paralleling the situation recorded both for *P. pelagicus* elsewhere (Williams 1982; Edgar 1990) and for other portunids (*e.g.* Hill 1979; Freier & Gonzales-Gurriaran 1995). The calcareous material found in the stomachs of *P. pelagicus* in Leschenault Estuary would provide the calcium required for the development of the exoskeleton of this species (Williams 1982). The diet of large crabs differed from that of small crabs in that it contained relatively greater amounts of polychaetes and relatively smaller amounts of amphipods. This difference is presumably related to the influence of an increase in the size of the chela and muscle mass on the type of prey that is most susceptible to predation (Freier *et al.* 1996) and to the greater ability of larger crabs to ingest larger prey such as polychaetes.

Portunus pelagicus in the Leschenault Estuary

The data presented in this paper on both the monthly trends exhibited by the size composition and abundance of crabs in Leschenault Estuary and Koombana Bay, when considered in conjunction with the time of spawning, have elucidated the broad details of the way in which *P. pelagicus* uses the Leschenault Estuary. Thus, after *P. pelagicus* has spawned in Koombana Bay, predominantly between the middle of spring and middle of summer, small numbers of the resultant 0+ age class start to become recruited into Leschenault Estuary in late summer and autumn. The numbers of this cohort decline in winter as salinities (and also water temperatures) fall to their lowest level, but then increase markedly as salinity and water temperature start rising sharply in mid-spring. The members of this cohort subsequently undergo rapid growth and, as a consequence, they typically attain maturity in late spring and summer when they are about one year old. Although female crabs apparently leave the estuary and enter Koombana Bay prior to or after becoming ovigerous, the fact that female crabs, which had undergone a pubertal moult, were present in the estuary during late summer and autumn, indicates that some female crabs do return to the estuary soon after spawning. However, male crabs are present in relatively greater numbers in the estuary during the same period, which indicates that they exhibit a greater tendency to remain in the estuary during this period. The larger crabs *i.e.* those representing the 1+ age class, are found in Leschenault Estuary until May and June, by which time they are *ca* 1½ years old. However, the majority of these larger crabs subsequently leave the estuary as salinities and also water temperatures fall to low levels in winter and, unlike the representatives of the 0+ cohort, rarely return as these two environmental variables start rising in the middle of spring. The significantly greater size of female than male crabs in crab pots in Leschenault Inlet parallels the situation found with another portunid, *Scylla serrata*, in Queensland (Williams & Hill 1982). Finally, our data show that, during its time in the estuary, *P. pelagicus* feeds predominantly on macrobenthic invertebrates and occasionally bottom-living fish.

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Sphaeromatid isopods (Crustacea: Isopoda) from the Leschenault estuary, Collie River and Bunbury Harbour

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Abstract

Seven species of sphaeromatid isopod were collected from the Leschenault area between 1995 and 1997. The Leschenault Estuary and the Collie River contain clearly estuarine species while Bunbury Harbour is dominated by introduced species. Changes in species diversity between 1995 and 1997 are documented. This is the first record of *Paracerceis sculpta* (Holmes 1904) for Western Australia. The most likely vectors of isopod introduction are recreational boats. It is suggested that sphaeromatid isopods can be used in estimating the frequency of introduction events.

Keywords: sphaeromatid isopods, crustaceans, estuary, Leschenault, Bunbury, south-western Australia.

Introduction

Sphaeromatid isopods lend themselves particularly well to describe and compare estuaries because their diversity and distribution reflect variations in hydrology and habitat (Hass & Knott 1998). Members of the benthic fauna, they have been generally neglected in estuarine studies and faunal surveys of the area (*e.g.* Chalmer & Scott 1984; Halse *et al.* 1989). It is therefore not surprising that, to date, only one study has recorded sphaeromatid isopods from the Leschenault system (Hass & Knott 1998). This investigation reveals that at least five species of sphaeromatid isopods colonize the area, with an additional two introduced species from Bunbury Harbour. The sampling area comprises three distinct sections: the Leschenault Estuary, a long shallow lagoon with a cut opening to the ocean; the mouth of the Collie River emptying into the estuary; and Bunbury Harbour, a small port with international and national shipping. It can be shown that these distinctions are again reflected in the sphaeromatid fauna. Moreover, the results presented here, combined with previous studies of the Swan River and other south-western estuaries, provide insights into the processes of introduction and spread of benthic fauna.

Materials and Methods

The Leschenault system was sampled on the 7 December 1995 and on the 1 and 2 October 1997. Ten sampling sites were chosen; two in the Leschenault Estuary, two in the Collie River (Fig 1, Table 1), and six in Bunbury Harbour (Fig 2, Table 1). All sphaeromatids were collected from hard substrate such as rocks, empty barnacle tests and dead wood within a vertical range of 5 cm below, to 1 m below, mean high tide level. Material from jetty piles was obtained using a pile scraper. For identification the specimens were preserved in 3.6% formalin/seawater mixture. Voucher specimens of *Paradella dianae* (Menzies 1962) (WAM C. 23302) and *Paracerceis sculpta* (Holmes 1904) (WAM C. 2303) have been deposited in the Western Australian Museum.

Results

Five species of sphaeromatid isopod were collected from the Leschenault area in 1997 but seven species colonized it in 1995. These species are; *Cymodetta gambosa* (Bowman & Kühne, 1974), *Exosphaeroma* sp, *Isocladus excavatus* Baker, 1910, *Sphaeroma quoyanum* (H Milne-

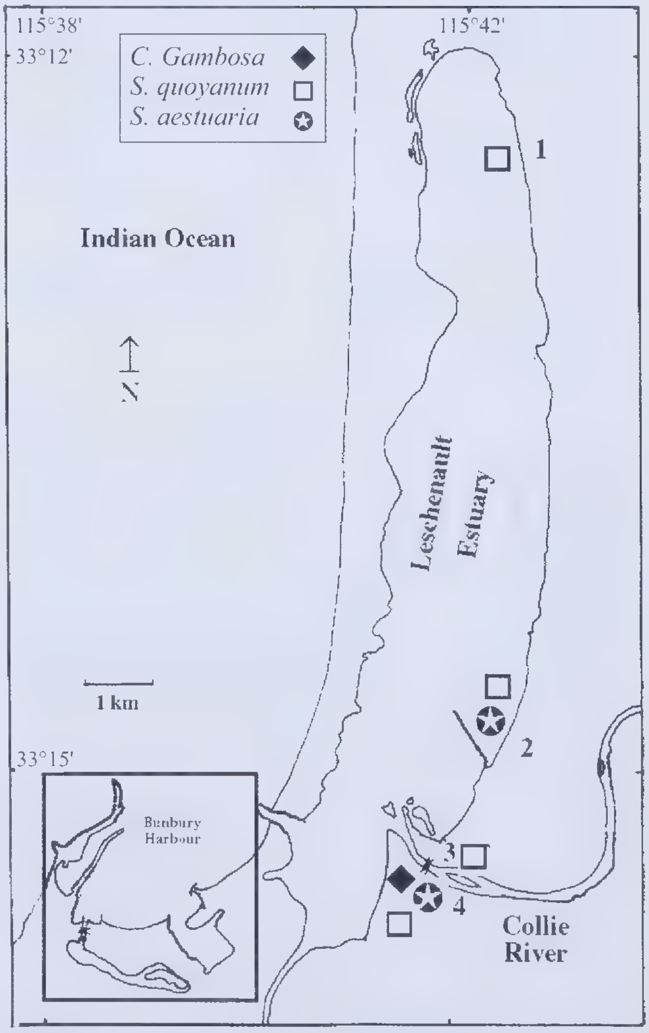

Figure 1. Distribution of sphaeromatid isopods in Leschenault Estuary and Collie River.

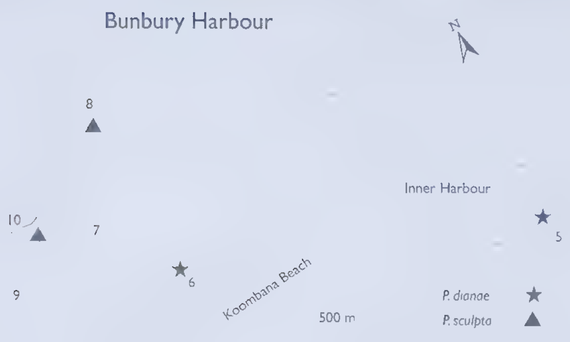

Figure 2. Distribution of sphaeromatid isopods in Bunbury Harbour.

Edwards 1840), *Syncassidina aestuaria* Baker, 1928, *Paracerceis sculpta* (Holmes 1904) and *Paradella dianae* (Menzies 1962). *Sphaeroma quoyanum, S. aestuaria* and *C. gambosa* define an estuarine environment. We found their occurrence restricted to the Leschenault Estuary and the Collie River, with *C. gambosa* occurring exclusively in the Collie River (Fig 1). Collecting in the estuary yielded only a few specimens while particularly *S. quoyanum* was found in great abundance on bridge piles in the Collie river. Overall, the species diversity and the availability of hard substrates as habitat is higher in the Collie River than the estuary. Bunbury Harbour, on the other hand, offers a great number of colonizable hard substrates mainly in the form of man-made constructions such as jetties and groynes. Two species, *P. dianae* and *P. sculpta,* were collected from these habitats (Fig 2). *P. sculpta* usually resides among algae, barnacles, ascidians and fanworms while *P. dianae* also colonizes the underside of rocks. Both species are known to be introduced to harbours around the world, but *P. sculpta* has not been reported before from Western Australia. The occurrence of *I. excavatus, Exosphaeroma sp* and *C. trilobita* in 1995 could not be confirmed in 1997 (Table 1).

Discussion

The results show that the sphaeromatid fauna clearly reflects its environment. The Leschenault Estuary and the Collie River harbour the estuarine species *S. quoyanum, S. aestuaria* and *C. gambosa.* These are known from the Swan River Estuary and *S. quoyanum* and *S. aestuaria* also occur in the Vasse and Hardy estuaries, with *S. quoyanum* being found in the Harvey Estuary as well (Hass & Knott 1998). This distribution indicates that they can all tolerate significant salinity changes. *Sphaeroma quoyanum* is the most widespread among them with the highest adaptability to the demanding estuarine environment. It is the only species that has been found in the Leschenault Estuary on both sampling occasions. *Syncassidina aestuaria,* only collected in 1997 when the salinity was 30 g L^{-1} as opposed to 40 g L^{-1} in 1995, can probably not persist in high salinities. As a lagoon with shallow muddy margins, high salinities in an estuarine context, temperature fluctuations in summer and limited amount of hard substrate, the Leschenault Estuary can only be inhabited by the most robust organisms.

Proceeding from the estuary into the Collie River, *C. gambosa* is added to the species list. In Western Australia it has been recorded from only one other site, the Swan River Estuary (Hass & Knott 1998). In both cases the populations are restricted to defined locations indicating that this species has quite rigid niche limitations or can be easily replaced by more dominant species. The extremely disjunct distribution, as well as no sightings in the Harvey, Vasse and Hardy estuaries, poses the question of its origin and history of spread.

Whenever harbours are included in faunal studies the identification of introduced species plays an important role because of their potential negative impact on native fauna and humans through reduction in diversity of indigenous species, release of poisonous metabolites, and damage to man-made structures such as jetties. Two of the species collected in Bunbury Harbour have been classified as introduced (Hutchings *et al.* 1987) but none has previously been recorded from this port in publications listing exotic species (Furlani 1996). *Paradella dianae,* first collected from Western Australia in Fremantle in 1978 (Harrison & Holdich 1982a), is known from the Arabian and Mediterranean Seas, California, Florida, Puerto Rico, Brazil and the east coast of Australia (Queensland). *Paracerceis sculpta* is similarly widespread. Its distribution includes the North American Pacific coast, the Mediterranean Sea and the east coast of Australia where it was collected from Townsville (Queensland) in 1975 (Harrison & Holdich 1982b). This is the first record of *P. sculpta* for Western Australia. Both *P. dianae* and *P. sculpta* are considered to travel in fouling communities on ship hulls which explains their occurrence in harbours around the world. There are two possible ways of introduction to Bunbury Harbour: organisms are carried by large vessels involved in either national or international trade, or by small recreational boats transferring the species from the port of first introduction to other locations. The fact that both species have been collected from small boat jetties indicates that recreational boating is a likely mechanism of spread between estuaries and harbours. Unpublished data by C Hass recording the presence of *P. sculpta* in a small boat harbour in Fremantle and on bridge piles in Mandurah, an estuary without commercial shipping south of Perth, support this argument. *Paradella dianae* is also reported from Fremantle but although still collected in 1995 its occurrence could not be confirmed in 1997 (C Hass, unpublished data), making Bunbury Harbour the only known location in Western Australia where this species is still abundant. However, a decline in numbers of *P. dianae* was noticed in 1997 after the remains of a small timber jetty with prolific marine growth had been removed from the harbour. It can be predicted that *P. sculpta* will also show a decline in numbers for the same reason. Aging timber constructions are probably the most important substrates for benthic organisms, both introduced and native, in harbours.

Movement of species between widely disjunct locations on the globe is a biological issue now well recognized as deserving careful attention (Vitousek *et al.* 1997). The potential impact of these species on Australian waters is not easily assessed because of the lack of previous documentation of isopod fauna. One effect may be that these introductions replace native species in the harbour environment. The disappearance of *C. trilobita, Exosphaeroma* sp and *I. excavatus,* species commonly occurring in the shallow littoral zone of

Table 1. Comparison of habitats, salinity and occurrence of Sphaeromatid isopods in the Leschenault Inlet area, 1995-1997

Station	Habitat	Salinity 1995 g L^{-1}	Salinity 1997 g L^{-1}	Species 1995 Data from Hass & Knott (1998)	Species 1997
Leschenault Estuary					
1	under rocks in empty barnacle tests	40	23	*S. quoyanum*	*S. quoyanum*
2	under rocks of retaining wall		30	not present	*S. quoyanum, S. aestuaria*
Collie River					
3	in empty barnacle tests on piles of bridge	16	10	*S. quoyanum, S. aestuaria*	*S. quoyanum*
4	under rocks, on dead wood	16	10	*S. quoyanum, S. aestuaria, C. gambosa*	*S. quoyanum, S. aestuaria, C. gambosa*
Bunbury Harbour					
5	under rocks on sandy beach		35	not present	*P. dianae*
6	under rocks of groyne		35	not present	*P. dianae*
7	under rocks of groyne	36		*I. excavatus, Exosphaeroma* sp	not present
8	from jetty piles among barnacles and ascidians		35	not sampled	*P. sculpta*
9	from jetty piles among fanworms, barnacles and ascidians	36		*P. dianae, C. trilobita*	not sampled
10	from jetty piles among fanworms, barnacles and ascidians		35	not sampled	*P. sculpta*

south-western Western Australia, from Bunbury Harbour and the absence of any of the native species in Fremantle Harbour provide strong support for this notion. Unlike the introduced fanworm *Sabella spallanzanii* (Gmelin 1791) with which the isopods co-occur, they have not been detected from any other environment indicating that their competitive advantage is restricted to ports. Whenever these sphaeromatids are found in harbours they most likely indicate other introductions such as algae, barnacles, bivalves and worms which may be more harmful and difficult to control. Since sphaeromatids show a decline in some places while other species persist and spread, their numbers may be able to reflect the frequency of introduction events and successful efforts to reduce introductions.

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Long-term spatial dynamics of polychaetes in Leschenault Inlet estuary

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Abstract

Long-term abundance and distribution changes of benthic polychaetes in the Leschenault Inlet estuary were monitored over a period of five years from February 1982 to May 1987. A total of fifteen polychaete species were recorded, one of which was a new species (*Ampharetidae* sp). Spatial distributions of the dominant species could be linked to environmental factors, particularly to salinity, water depth and substrate. These specific habitat preferences indicate three polychaete assemblages. Long-term abundance changes of the three most common species, *Ceratonereis aequisetis, Nephtys gravieri* and *Capitella* cf *capitata*, followed rather complex patterns. Average circa-annual periodicity in abundance at a single site was typically unimodal, with a peak in late summer to autumn. There was no obvious circa-annual periodicity for the overall populations of given species, probably because large year-to-year variability at single sites and phase differences between sites masked the average pattern. Coincident long-term trends observed for *C. aequisetis* at neighbouring sites revealed a persistent synchronicity after disturbance, but a lack of coupling to seasonal variation in abiotic factors. This suggests the spatial and temporal changes in polychaete distribution within the Leschenault Inlet estuary mostly reflect local scale environmental conditions.

Keywords: estuarine polychaetes, Leschenault Inlet, estuary, south-western Australia.

Introduction

Few studies of estuarine macrobenthic infauna have been carried out in Western Australia, hence the polychaete fauna is poorly known (Hodgkin & Clark 1987-1990; Phillip & Lavery 1997; Platell & Potter 1996). Augener (1913, 1914) lists about 160 species of polychaetes from south-western Australia. Although most specimens were collected from marine sites, there are a few important estuarine records contained in this work. Hodgkin & Clark (1987-1990) compiled polychaete fauna lists for estuaries in south-western Australia from recent literature records and from cursory collection of material from locations where no previous work had been carried out. The latter inventory provides a taxonomic working-list with some 20 estuarine species of polychaetes noted for estuaries in the southwest region. Only three previous studies specifically identified polychaetes from the Leschenault Inlet estuary; Anon (1983) identified three species of polychaete, Chalmer & Scott (1984) recorded six species, and Deeley (Murdoch University *pers. comm.* 1998) recorded 13 species, six of which were identified only to the family level.

However, very little is known about estuarine polychaete biology and autecology apart from their presence at particular sites. Ecological studies investigating the preferences of particular polychaete species for various substrates and salinity ranges within estuarine environments of Western Australia are even sparser. Notable exceptions are the works by Platell & Potter (1996) at Wilson Inlet and Phillip & Lavery (1997) at Waychinicup estuary. Long-term studies that allow assessment of circa-annual patterns in the population dynamics of particular species over several years have not been carried out in Western Australia.

A number of long-term studies on polychaete population dynamics, however, have been carried out in both marine and estuarine environments (*e.g.* Hutchings 1984; Kaleijta 1992; Beukema *et al.* 1993), but usually the reported temporal patterns can not be easily linked to environmental factors present in different habitats. This paper specifically attempts to address this problem within the context of the Leschenault Inlet estuary in south-western Australia, because of the high-resolution spatial and temporal sampling over several years. We provide an inventory of species compiled from five years of sampling benthic polychaete infauna of the Leschenault Inlet estuary. Moreover, we correlate polychaete distribution patterns to environmental factors, and show the temporal and spatial fluctuations in abundance and distribution of the three main species found in this estuary on short to long-term time frames.

Methods

Regional setting

Physical, chemical, habitat, and sedimentological aspects of the Leschenault Inlet estuary are described in Semeniuk V (2000) and Wurm & Semeniuk (2000). These studies document the range of estuarine habitats along four cross-inlet transects, which provide representative shallow and deep water sites in each of the four salinity fields of this estuary (Transects A-D; Fig. 1). Since the polychaetes described in this study were collected along the same transects, only a brief description of the range in salinity, substrate and aquatic vegetation along these transects is reiterated here. Salinity regimes are described after the Venice system for brackish waters (Anon 1959).

Transect A (sites A1-7) was located in the deltaic salinity field, where salinity varied from mesohaline in winter to euhaline in summer. Substrates comprised sands in shallow areas and sandy mud in the deeper basin area (sites A4 and A5). Most sites had the seagrass *Halophila ovalis* present (except sites A1 and A2 located on the delta front). Green (*Acetabularia, Chaetomorpha*), red (*Gracilaria*) and brown algae (two unidentified species) also were present at sites A5, A6 and A7.

Transect B (sites B8-14) was located in the lower estuarine salinity field, where salinity was euhaline throughout the year. Substrates were sandy in shallow regions on the western and eastern margins, with mud present in the deeper basin region (sites B11 and B12). *Halophila* was present at all sites, although in low abundance at sites B11 and B12. Algae were only found at sites B13 and B14 on the western margin.

Transect C (sites C15-19) was located in the mid-estuarine salinity field, where salinity was polyhaline in winter and euhaline in summer. Substrates comprised sandy mud on the eastern margin and were muddy in the deeper basin and western margin regions. *Halophila* was present at all sites. Algae occurred along the shore margins.

Transect D (sites D20-22) was located in the upper estuarine salinity field, where salinity was polyhaline in winter and hyperhaline in summer. Substrates were typically mud-dominated. Algae occurred patchily at all sites.

Methodology

Polychaetes were identified and counted from samples collected during seasonal benthic surveys of the Leschenault Inlet estuary in the years 1982-1987. Samples were collected quarterly at 22 sites along Transects A-D from May 1982 to May 1987 (Fig. 1 B, C). Additionally, eleven of these sites (sites

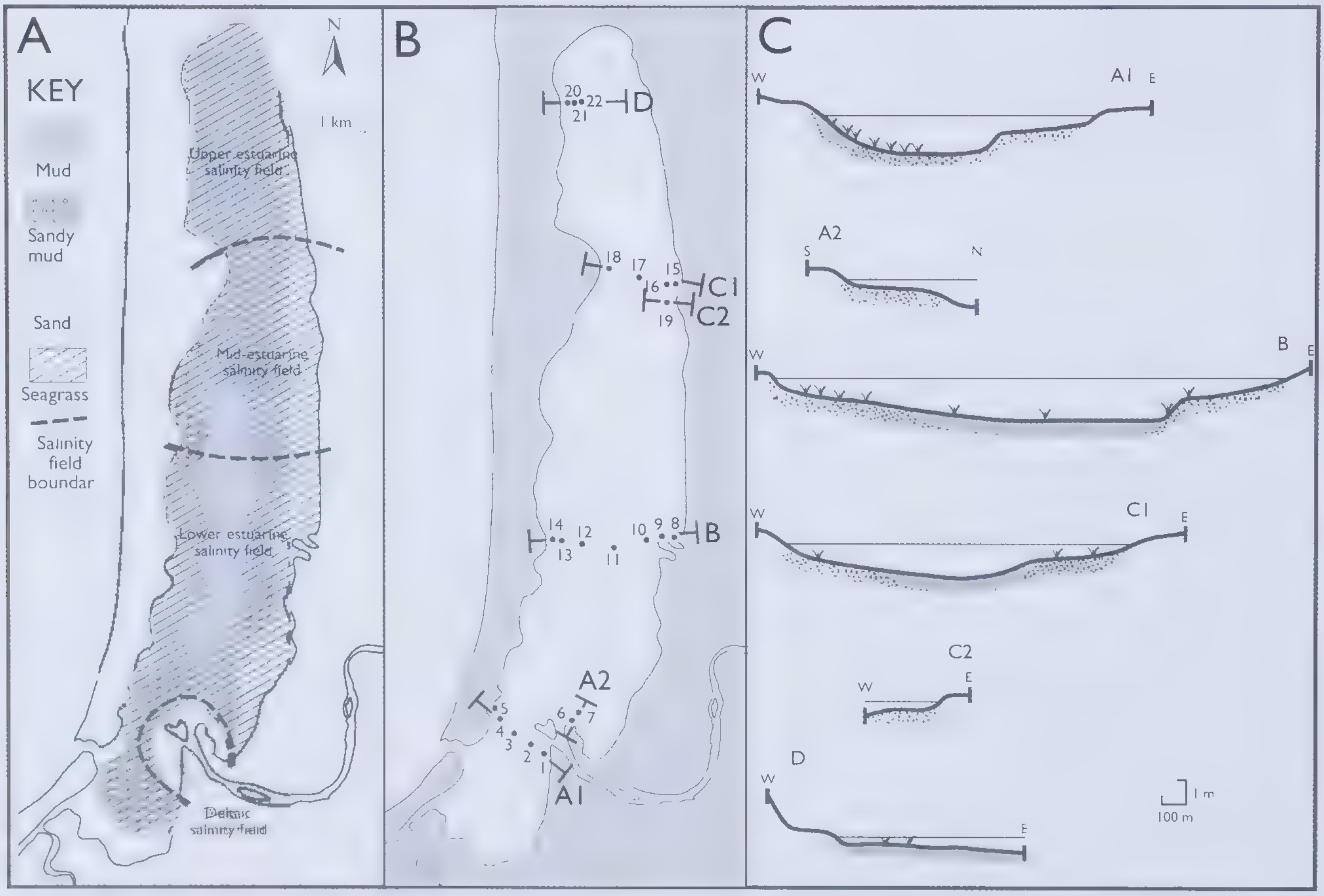
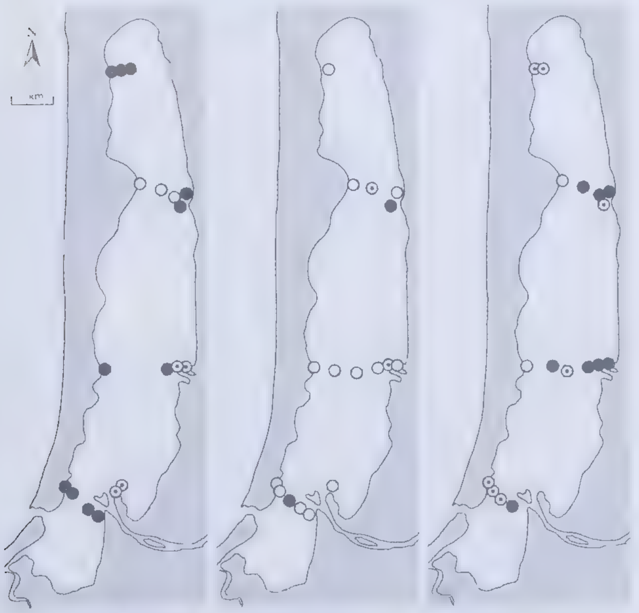


Figure 1. A: Habitat framework of Leschenault Inlet estuary after Wurm & Semeniuk (2000) with superimposed distribution of the seagrass *Halophila* after Lukatelich (1993). Major determinants of habitat classification are salinity regime (deltaic, lower, mid- and upper salinity field) and substrate composition (sand, muddy sand, sandy mud, mud). **B:** Sampling transects and sites in Leschenault Inlet estuary. Four transects were chosen according to prior habitat classification by Wurm & Semeniuk (2000). Transects A, B, C and D run across the deltaic/lower, lower estuarine, mid-estuarine and upper estuarine salinity fields, respectively. **C:** Schematic cross-sections are redrawn after Wurm & Semeniuk (2000). Seagrass is recorded only at sampling sites. Dots (sand) and grey shading (mud) indicate substrate type.

A2, A3, A4, B9, B11/12, C15, C17, C19, D20, D21 and D22) were monitored monthly during the period May 1986 to May 1987 as part of a more detailed faunistic study (Wurm & Semeniuk 2000). Each site was sampled by retrieval of five randomly placed sediment cores; each core was 78.5 cm^2 in surface area and 15 cm depth. In May 1982, 10 samples per site were taken. The core was sieved with a 1 mm mesh. Retained specimens were immediately fixed in formaldehyde and fragments of menthol were added for the first few hours after collection in order to make the polychaete mouthparts accessible. Later, samples were washed and subsequently stored in 10% phenoxytol solution. More detailed information about the sampling strategy and sampling history is given by Semeniuk & Wurm (2000).

Specimens were identified and counted from each sample. However, field sieving, heat exposure, storage time and either the persistence of menthol in samples or insufficient fixation resulted in preservation problems for a number of samples. Deterioration of specimens in samples from August 1982 limited identification of species to those possessing chitinous mouthparts *e.g.* families Nereidae and Nephtyidae. Minor deterioration of specimens also occurred in May and December 1982. These circumstances affected the data on temporal variation and quantitative analyses of *Capitella cf capitata* for August 1982, and to a lesser extent for the sampling times of May 1982 and December 1982. Some problems with identification were also encountered due to fragmentation of the specimens during sieving, especially for *Capitellidae*, where setae patterns along the body length are important. In spite of the large sample base underlying this study, it is therefore possible that the reported species list is not exhaustive.

Additional samples collected in 1997 were used to provide fresh material for taxonomic work. Taxonomic reference standards were established using the keys and species descriptions of Augener (1913, 1914), Day (1967), Rainer & Hutchings (1977), Hutchings & Murray (1984) and Hutchings & Glasby (1985). Some of our reference standards were cross-checked by P Hutchings (Australian Museum). Comparison of our reference standards with sample material enabled identification of most specimens.



Ceratonereis aequisetis Nephtys gravieri Capitella capitata

Figure 2. Distributions of the three main polychaete species of Leschenault Inlet estuary, based on maximum abundance at monitored sites between 1982-1987. Abundance is depicted for each site and rated as 'very common' (● > 10 specimen per site), common (⊙: 5-10 specimens per site) and uncommon (○: 1-5 specimens per site).

Statistical analyses were attempted using a general linear model with replication (SPSS V8.0). The five sampling years and four sampling seasons were selected as 'inner subject' factors, with substrate (sand, muddy sand, sandy mud and mud), salinity (estuarine, lower, mid- and upper salinity field) and depth (intertidal and subtidal) as 'between subject' factors. However, due to the large number of samples containing no specimens, data distributions were highly skewed and even after square-root transformation were not normal-distributed according to Kolmogorov-Smirnov and Shapiro-Wilk Tests. Moreover, neither Levene's Test for homogeneity of variances, nor Mauchly's Test for sphericity were significant. This suggests the data were not suitable for analysis of variance. As a consequence, statistical analysis was limited to calculation of mean and standard error. Mean species abundance and standard error are always given for the sample area of a single core (except for Fig 7). Mean species abundance for the core area can be converted to species abundance per square meter by multiplying by 127.4. Thus abundance is used synonymously to population density.

Results

Inventory of species and diversity

Fifteen polychaete species were recorded for the Leschenault Inlet estuary in this study (Table 1). Most species were recorded over the interval 1982-1987 with three additional species recorded only in 1997. *Ampharetidae* sp represents a new species, possibly even a new genus (P Hutchings, Australian Museum, *pers. comm.*), but preservation was not adequate for an original description. The preservation state of the delicate Phyllodocidae also did not allow us to distinguish between the genera Phyllodoce and Anaitides, both of which have been recorded from south-western Australian estuaries before. To our knowledge, *Glycera* cf *americana* and *Lumbrineris* cf *latreilli* were recorded for the first time from Western Australia.

Table 1. Polychaete species list for Leschenault Inlet

Name	Family
Amplaretidae sp	Ampharetidae
Capitella cf capitata (Fabricius 1790)	Capitellidae
Mediomastus sp*	Capitellidae
Caulleriella sp*	Cirratulidae
Glycera cf *americana* (Leidy 1855)	Glyceridae
Lumbreineris cf *latreilli* (Adouin and Milne-Edwards 1834)	Lumbrineridae
Nephtys gravieri (Augener 1913)	Nephtyidae
Australonereis ehlersi (Augener 1913)	Nephtyidae
Ceratonereis aequisetis (Augener 1913)	Nereidae
Neanthes oxypoda (Marenzeller 1879)	Nereidae
Diopatra dentata (Kinberg 1865)	Onuphidae
Scoloplos simplex (Hutchings 1974)	Orbiniidae
Harmothoe praeclara (Haswell 1883)	Polynoidae
Phyllodoce or *Anaitides* sp	Phyllodocidae
Prionospio cf *cirrifera* (Wiren 1883)*	Spionide

* recorded in 1997 only.

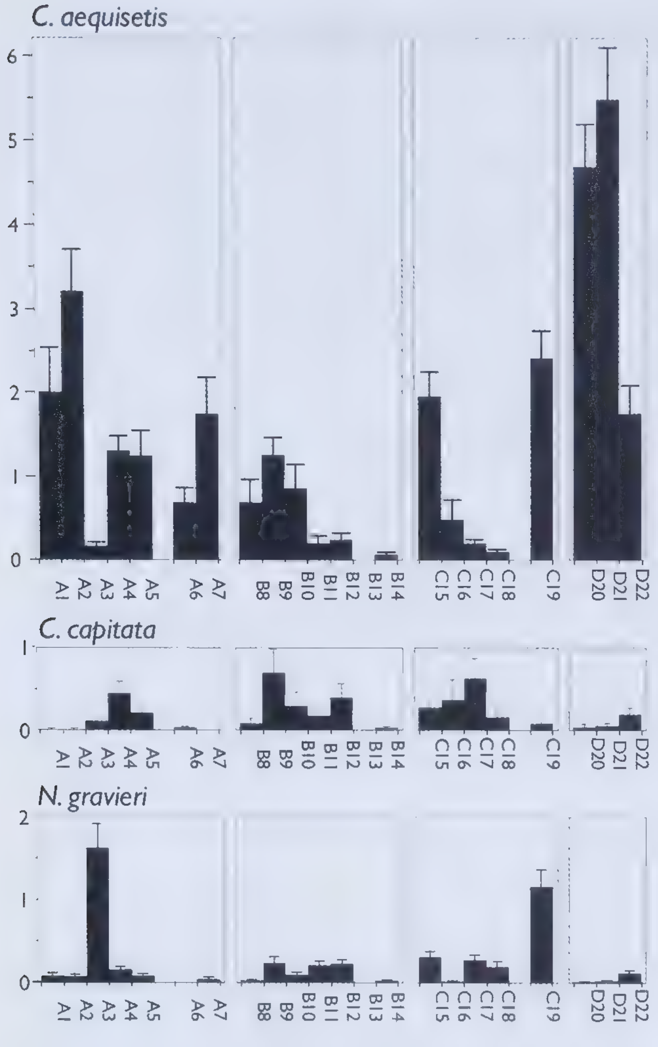


Figure 3. Average abundance of the three main polychaete species of Leschenault Inlet estuary between 1982 and 1987. Values are mean number of specimens per sample ± standard error for *C. aequisetis*, C. cf capitata and *N. gravieri*, for each site along the four transects (n=140 for sites A2, A3, A4, B9, B11, B12, B14, C16, C18, C19, D20, D21 and D22, otherwise n=105). Spacing of bars within the 1st and 3rd columns separate sub-transects A1-5, A6-7 and C15-18, C19.

Over the period of the study, the most abundant species in the Leschenault Inlet estuary were *Ceratonereis aequisetis, Nephtys gravieri* and *Capitella* cf *capitata*. *Scoloplos simplex* was also commonly recorded in samples from sandy regions of the lower and middle estuary. Other species were recorded only rarely or only in 1997.

Overall species diversity for this estuary was low and samples were typically mono-specific. Highest diversity was recorded along Transect A where up to five species per sample were retrieved from deep basinal mud of the lower estuarine field (site A4; see Fig. 2). Diversity decreased from the lower estuary towards the upper estuarine regions. The upper estuarine field was dominated by a single species, *C. aequisetis* (see Fig. 2).

Spatial patterns of species

Quantitative analyses of spatial and temporal abundance change were restricted to the three main species of the Leschenault Inlet estuary, *C. aequisetis, N. gravieri*, and *C.* cf *capitata*. All other species occurred too patchily or infrequently to give a reliable account of their spatio-temporal population dynamics. For the three main species, maximum abundance at a given site was used as an indication of the maximal extent of their distribution within the estuary (Fig. 2). Additionally, mean abundance of these species was plotted along each transect to display average distribution for a given site (Fig. 3).

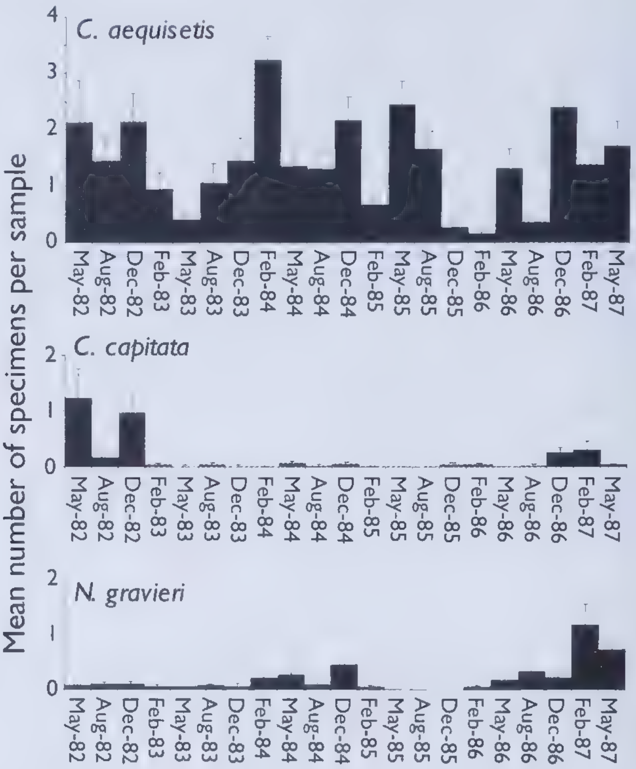


Figure 4. Overall mean abundance of the three main species indicates total biomass attributed to a single polychaete species through time. Species counts were pooled for all sites at a given month. Only quarterly samples are calculated for 1986-1987. Values are mean ± standard error.

Ceratonereis aequisetis was recorded at all but one of the 11 sites monitored monthly. Highest abundances were recorded on the upper estuarine mud flat at sites D20-22 (Transect D), where there were up to 50 individuals per sample. Maximum abundance (Fig. 2) indicates that this species was very common at shallow sandy sites A1 and A2 in the Collie Delta region, sites C15 and C19 on the mid-estuarine eastern platform and shallow sandy mud (B14) or muddy sand sites (A4, A5, B10) of the lower estuarine region. *C. aequisetis* was common *i.e.* 2-5 individuals per sample maximum, at other sites in the Collie Delta region (sites A6, A7) and at shallow sandy and muddy sand sites in the lower estuarine region (sites B8, B9). *C. aequisetis* appeared to favour shallow and intertidal regions of the estuary with no specific preference for sediment type. Average abundance along transects reflected this preference for shallow sites (Fig. 3), since the species typically showed a drop in abundance with increasing depth along a transect (*e.g.* C15, C19 *vs* C16; D20, D21 *vs* D22). This pattern was most pronounced along Transect D, where the species was by far the dominant taxon. At the shallow site D21, mean abundance was more than 100 times those of *C.* cf *capitata* and more than 300 times those of *N. gravieri* in the intertidal mud, whereas the relative dominance of *C. aequisetis* was reduced by a factor of ten at the slightly deeper water site D22. The decrease in abundance of *C. aequisetis* was paralleled by an increase in abundance of the other two species. Interestingly, in sandy sites of the deltaic region (along Transect A) this relationship with depth was reversed (Fig. 3), with lower abundances of *C. aequisetis* in the shallow intertidal zone than in the deeper subtidal zone (*e.g.* A2 *vs* A1; A7 *vs* A6). This reversal may have been due to the effect of freshwater input at these sites, or to the absence of seagrass. Since this species occurred throughout the lower to upper estuarine salinity fields, the latter explanation is more likely.

Capitella cf *capitata* was recorded at all but one of the 11 sites monitored monthly, but occurred most commonly within the lower and mid-estuarine salinity fields sampled along Transects B and C (Fig. 2). Highest abundances were recorded at sites B9 and C17, with up to 20 individuals per sample. *C.* cf *capitata* was abundant in lower to mid-estuarine basinal mud and less abundant on the adjacent eastern sandy platform and western muddy platform (Fig. 3). *C.* cf *capitata* was rare on both the deltaic front and on the upper estuarine muddy flat. It had a salinity preference for the lower to mid-estuarine fields and to favour mud or muddy sand substrates.

Nephtys gravieri was not recorded at all sites (Fig. 2). It was notably uncommon or absent in the deltaic region (sites A1-2, A6-7) and upper estuarine region (sites D20-22), and sparse at shallow muddy sites on the western platform (B14, C18). Mean abundance was highest at basinal sites of the lower and mid estuarine region (A3, B10-12, C17) and at sandy sites along the western platform margin of the lower and mid-estuarine field (B9, C15, C19). *N. gravieri* reached highest abundance at the lower estuarine basin site A3, with up to 20 individuals per sample. From these data the species appeared to have no clear preference for substrate or depth, but preferred the stable salinity regime of the mid-estuarine region.

Scoloplos simplex was recorded mainly at sites A1, A6-7, B8-10 and C19, which correspond to sandy areas of the eastern platform margin (data not shown). Abundances were typically 1-2 individuals per sample. It was notably absent from the upper reaches of the estuary, and appeared to favour intertidal sandy sites of the lower to middle estuary.

The distributions of the remaining polychaete species were more difficult to delineate, since their low abundances did not always guarantee collection during the various sampling surveys. *Ampharetidae* sp was only recorded along Transect D at sites D21 and D22. *Glycera* cf *americana* was recorded only from muddy sand on the lower estuarine western platform (site A4). *Lumbrineris* cf. *latreilli* was recorded in the lower estuarine field at sandy mud and muddy sand sites A3-5. *Australonereis ehlersi* was recorded at sites A1-4, B11, C15 and C17, which are sand, muddy sand and mud sites in the lower to mid-estuarine fields. Low numbers of *Neanthes oxypoda* were consistently recorded at sites A2 and A4. *Diopatra* cf *dentata* was recorded from deep basinal mud at site A3. *Harmothoë praeclara* was recorded at most muddy sand sites of the eastern platform (B9, B10, and C16) and at site A4. *Phyllodocidae* sp was only recorded from basinal mud at sites A3, A4 and B11/12 in the lower estuarine field. *Prionospio* cf *cirrifera*, *Mediomastus* sp and *Caulleriella* sp were only recorded in 1997 at sites C15 and C17 on the eastern platform margin within the mid estuarine region.

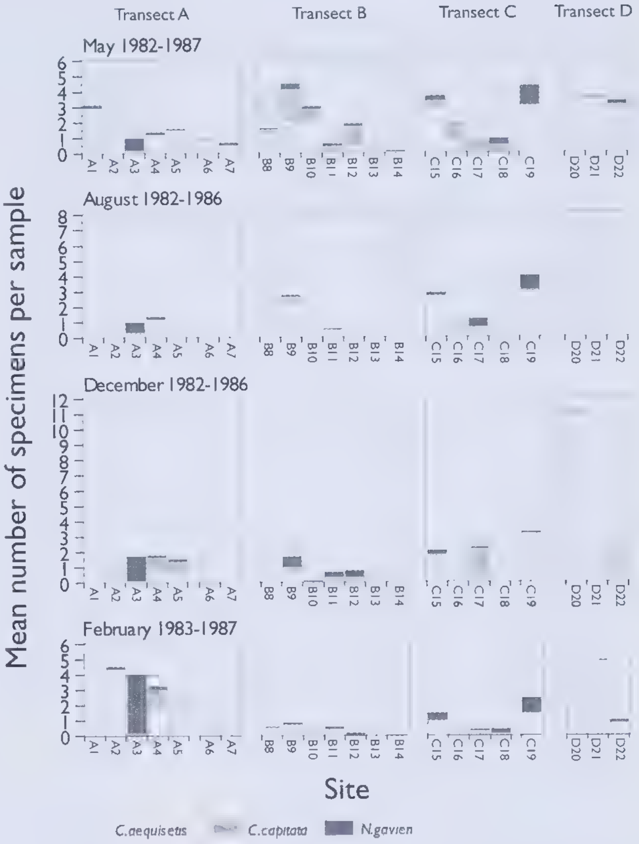


Figure 5. Average seasonal change in abundance of the three main species. Mean species abundance was pooled for a given season, but calculated separately for each site. Site data are arranged in columns, corresponding to sampling transects. Spacing of bars within the 1st and 3rd column separate sub-transects A1-5, A6-7 and C15-18, C19.

Long-term abundance

To present a measure of the overall biomass attributable to a given species of polychaete and its change through time, the temporal sequence of mean species abundance was examined (Fig. 4). There was no consistent circa-annual pattern over the five-year sampling period for any of the three main species. Mean species abundance of *C. aequisetis* showed some periodic change, in that for four out of five years it was lower in February than in December, and again lower in August than in May. However, the amplitude of the fluctuation was of the same order of magnitude as the underlying putative pattern, so variability masked any consistent periodicity.

Seasonal abundance

Average species abundances over the five years for the months of May, August, December and February for each site (Fig. 5). were typically a unimodal circa-annual pattern for each of the three main species at single sites. However, it is evident from comparing different sites that

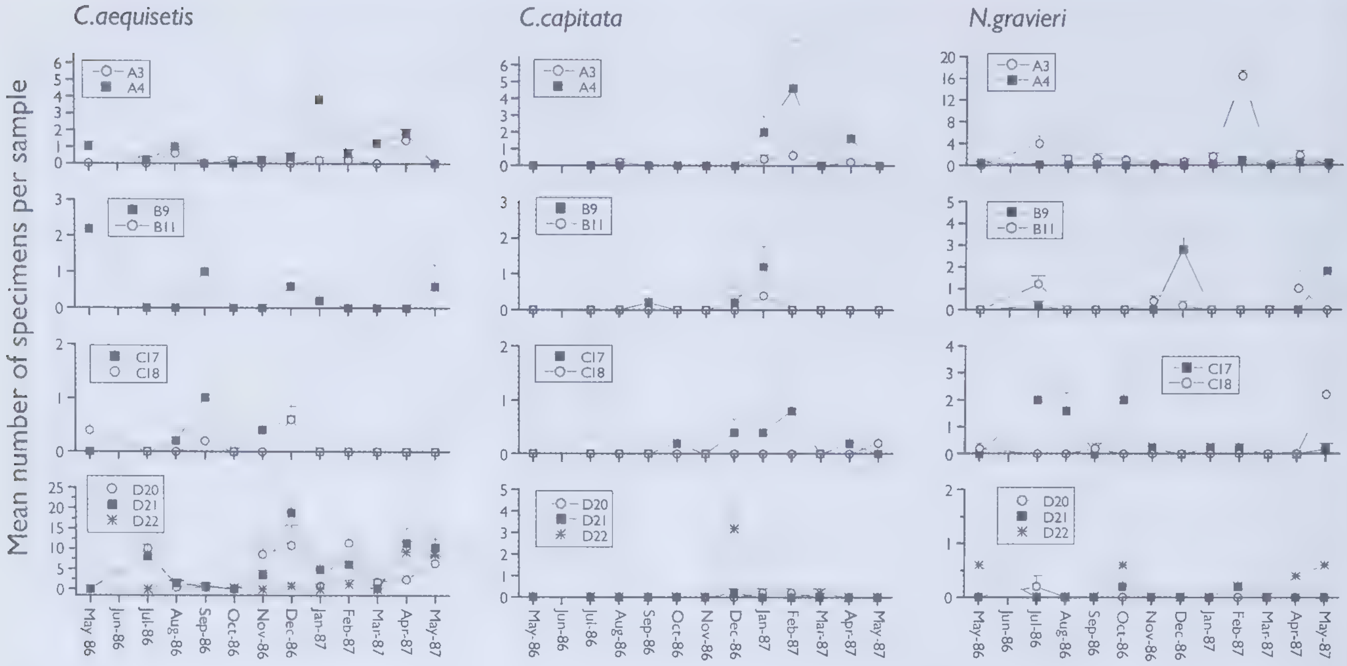


Figure 6. Temporal variation of species abundance on a monthly basis from May 1986 to May 1987. Mean species abundance per sample was calculated for nine sites and grouped according to transects (rows) and species (columns). Values are mean ± standard error; note different scales of the ordinates.

the maximum of this unimodal pattern occurs in different months. For example, average abundance of *C. aequisetis* reached a maximum in December at upper and mid-estuarine sites D20, D21 and C17; in February at deltaic and lower estuarine sites A2, A4, A5 and A7; in May at lower and mid-estuarine sites B8-10, B12, C15, C16, C19), but also at deltaic and upper estuarine sites A1, A6 and D22 (Fig. 5). At sites dominated by other species, it appears the average abundance of *C. aequisetis* may even have peaked in August, when the dominant species was least abundant (*e.g.* specimen numbers of *C. aequisetis* were anti-cyclic with *N. gravieri* at A3, and *C.* cf *capitata* at B11; Fig. 5). Similar observations could be made for the other two species.

The magnitude of abundance changes varied significantly between sites. At some sites, seasonal changes were relatively small (*e.g. C. aequisetis* at A2; Fig. 5), whereas at nearby sites populations varied from a moderate abundance of 1-2 individuals per sample to total absence (*e.g. C. aequisetis* at site A7; Fig. 5). Highest abundances were recorded in February or May at most sites *i.e.* late summer to autumn. It is obvious that the varying amplitudes and phase shifts of local, unimodal dynamics are unlikely to superimpose into a simple circa-annual pattern (Fig. 4). Hence, two questions emerge; (1) how variable were seasonal abundance changes at a given site within a single year *i.e.* could more frequent sampling reveal more complex patterns?; and (2) how variable were these seasonal patterns from year-to-year *i.e.* is the average seasonal pattern long-lasting and consistently present?

Short-term spatio-temporal variation

To address the first question, circa-annual abundance changes were examined for nine sites sampled monthly from July 1986 to May 1987 (Fig. 6). In some cases, such as for *C. aequisetis* at upper estuarine sites D20-22, monthly changes of abundance were remarkably similar (Fig. 6). There were also several instances of concurrent abundance peaks at different sites along the same transect for a given species, as well as concurrent abundance peaks for different species at the same site. For example, abundance of *C. aequisetis* had coincident local maxima in December 1986 at sites B9, C17, C18, and D20-22 (Fig. 6). In this month, coincident peaks were recorded for *N. Gravieri* at site B9 and *C.* cf *capitata* at site D22. Other months typically showed fewer coincidences of peaks. Peak abundances for *C.* cf *capitata* almost always occurred between December and February at all of the nine sites, a pattern that was less pronounced for *C. aequisetis* and *N. gravieri* (Fig. 6). Hence, it appears that circa-annual abundance patterns varied a great deal between sites and between species, although there were some coincident short-term trends.

Long-term spatio-temporal variation

To address year-to-year variability, quarterly species abundance was plotted for four sites of the western platform and three sites of the central basin (Fig. 7). Sites were grouped such that they show a transition through different salinity fields at different depths (*i.e.* a deep-water and a shallow-water site from each Transect A-D). All sites had muddy substrates.

The long-term temporal variation of abundances at these sites showed both coincident events and pronounced variability, similar to the observations made for the one-year cycle (Fig. 6). Generally, year-to-year variability between samples of the same month was enough to mask the average unimodal pattern (Fig. 5), but some long-term trends could still be recognised at different sites for particular species. For instance, there were periods of high abundance of *C. aequisetis* at sites A4, B11, C17 and D22 from February 1984 to August 1985 (Fig. 7). A similar trend

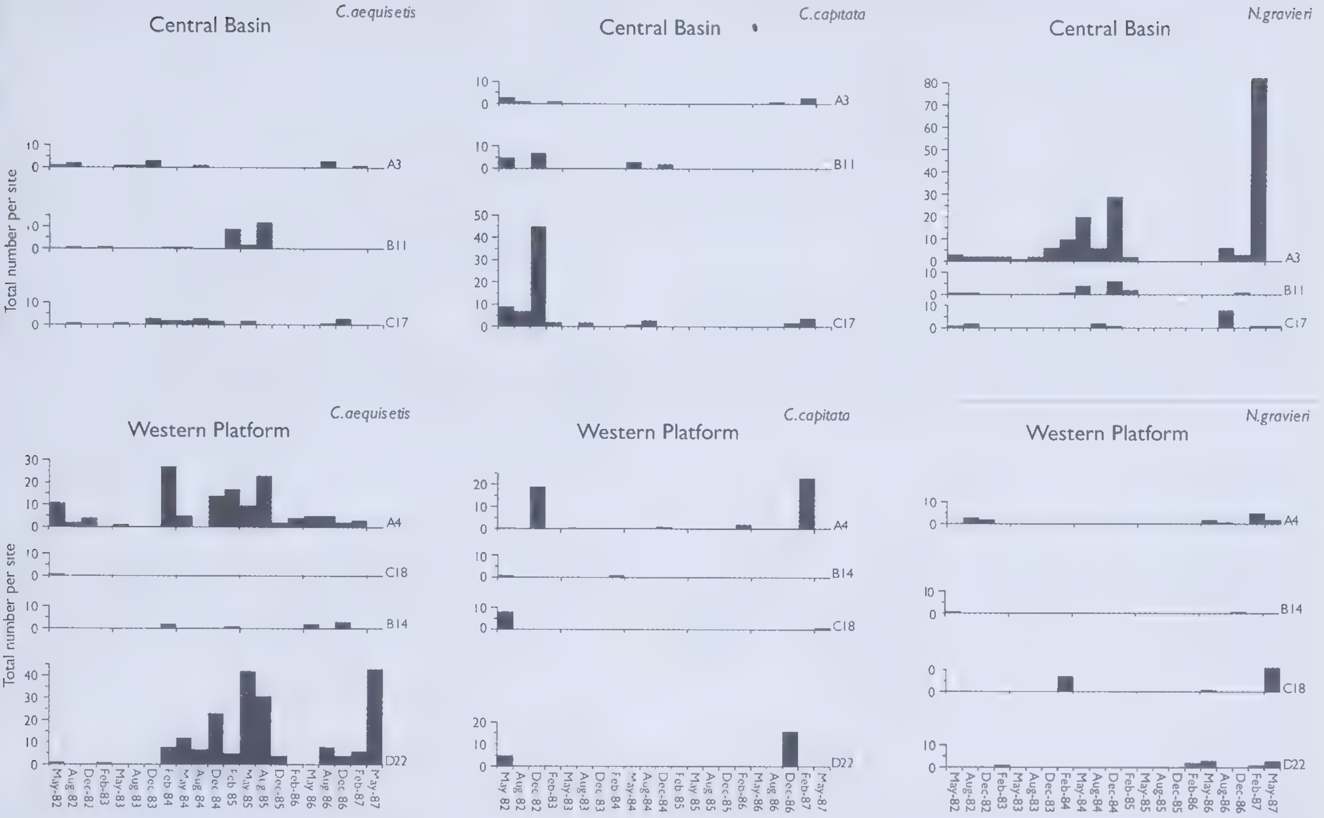


Figure 7: Long-term temporal variation of species abundance on a quarterly basis from May 1982 to May 1987. Total species counts from five samples per site and date, were calculated for seven sites. These are grouped according to depth (rows), salinity (sequence within single box) and species (columns).

was observed for *N. gravieri* at sites in the central basin; coincident peaks could be seen during May 1982 to December 1982 and December 1986 to February 1987. *N. gravieri* exhibited only irregular peaks at site A3 in 1984 and 1986/87. These peaks appeared to post-date mesohaline periods at site A3, suggesting that this was either a population stress response or an opportunistic response to fluctuating environmental conditions, or due to mass mortality of other species. The grouping of sites again emphasises the preference of species for particular habitats; *C. aequisetis* was most abundant at shallow-water sites of the lower to upper estuary; *N. gravieri* was most abundant at deep-water sites of the lower estuary; and *C.* cf *capitata* had peak abundance in the mid-estuarine basin, but occurred with moderate abundances in both lower and upper estuarine sites of the western platform.

Small-range spatial changes of species.

Small-range spatial fluctuations in a single species population were investigated for the *C. aequisetis* along Transect D (Fig. 8). Mean abundance changes along Transect D were mainly determined by the population dynamics occurring at sites D20 and D21. However, the periodic pattern of the initial two years of sampling was markedly different at these two sites. In 1982 and 1983 the abundance of *C. aequisetis* at site D20 showed a single prominent peak each year (December collections), while the abundance at site D21 peaked four months earlier (August collection) and settled down to a medium level for the following six months (December and February collections).

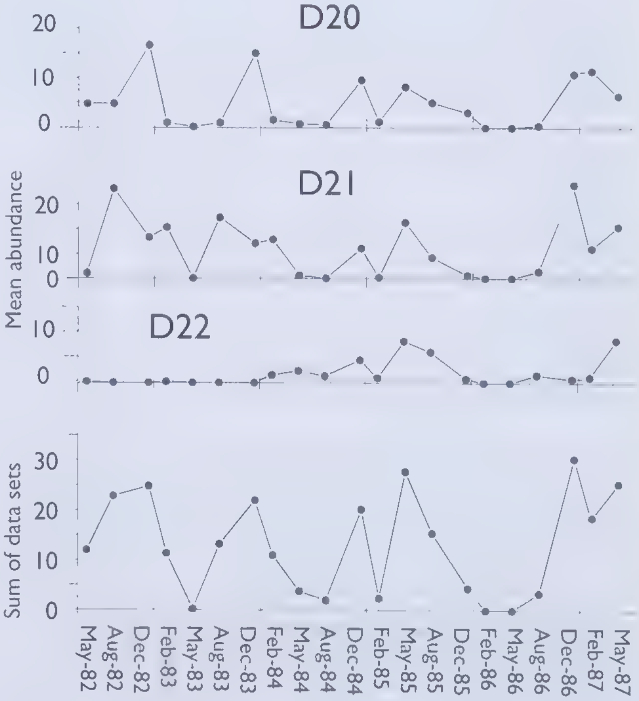


Figure 8. Temporal abundance change of *C. aequisetis*, recorded over a sequence of five years. Values are mean ± SE for five replicate samples collected at sites D20-22 from the upper estuary. The bottom panel shows the sum of the three data sets.

The earlier rise and broader base of this second peak may reflect spreading of the *C. aequisetis* population from the more central regions of the mud flat near site D21 towards site D20. Changes to this circa-annual pattern occurred post-February 1984, with a notable increase in abundance changes at site D22. A sharp 'disturbance' in February 1985 characterised by a drop in abundance was recorded at all Transect D sites. The following peak and trough in 1986 was also observed at all sites. The circa-annual pattern of the years 1982 to 1984 were synchronous with marked salinity and temperature changes that occurred in the upper estuarine flat (Wurm & Semeniuk 2000). However, the decrease in abundance in February 1985 lacked a corresponding change in abiotic factors.

Discussion

Faunal composition

Our record of fifteen benthic polychaete species for the Leschenault Inlet estuary appears to be rather low given the mainly euhaline marine environment of this estuary, particularly when compared with polychaete diversity in estuaries of New South Wales (Hutchings & Murray 1984) or South Africa (Day 1981), where over 200 species have been recorded. However, our records are comparable with the fourteen species recorded from Wilson Inlet by Platell & Potter (1996) and agree well with the total species number for south-western Australian estuaries (Hodgkin & Clark 1987-90). The relatively low polychaete diversity may be due to the absence of seagrasses from the family Potamogetonaceae (*Posidonia, Zostera, Ruppia*). *Posidonia* meadows in the Hawkesbury River and other southern estuaries of New South Wales are the habitat most preferred by polychaetes (Hutchings & Murray 1984). Similarly, the presence of eelgrass *Zostera* affects diversity or abundance of benthic polychaete fauna both in South Australian estuarine (Conolly 1997) and marine environments (Hutchings *et al.* 1993). Platell & Potter (1996) also report a significant positive correlation of species diversity and the presence of *Ruppia megacarpa*. Whether seagrasses from Hydrocharidaceae, such as *Halophila* lack this positive effect on polychaete diversity remains to be investigated. A second factor possibly contributing to low diversity in our study area was the shallow sampling depth of 15 cm. Deeply burrowing species might have been missed or inadequately sampled in our study. For example, the deeply burrowing eunicid *Marphysa sanguinea* recorded for the Swan-Canning-System (Thurlow *et al.* 1986) was not recorded in our study.

All species listed in Table 1, with the exceptions of *Ampharetidae* sp, *Glycera* cf *americana, Lumbrineris* cf *latreilli* and *Nephtys gravieri*, have been previously recorded from the Leschenault Inlet estuary (*e.g.* Anon 1983) or from other estuaries from south-western Australia (Hodgkin & Clark 1987-1990). The most dominant benthic polychaete species found throughout the Leschenault Inlet estuary during this study, was *C. aequisetis*. Both *N. gravieri* and *C.* cf *capitata* had moderate local abundances. The only other species frequently recorded was *S. simplex*. Except for *N. gravieri*, these species also are dominant benthic components in other south-western Australian estuaries including Wilson Inlet, Wellstead Inlet, Broke Inlet and Beaufort Inlet (Hodgkin & Clark 1987-90; Platell & Potter 1996). Surprisingly, *N. gravieri* has never been listed for south-western Australian estuaries, although it was originally described from a marine site off Fremantle (Augener 1913) and could easily migrate into local estuaries.

There were a number of notable differences between the polychaete fauna of other south-western Australian estuaries and the Leschenault Inlet estuary. Polychaete families that are absent from Leschenault Inlet estuary but are found in other south-western Australian estuaries include Eunicidae (Swan-Canning System; Thurlow *et al.* 1983), Arenicolidae (Wilson Inlet; Hodgkin & Clark 1987-90), and Opheliidae, Sabellidae and Hesionidae (Wilson Inlet; Platell & Potter 1996). For example, *Boccardia chilensis* and *Heteromastus filiformis* are both very common in Wilson Inlet, but were not found in Leschenault Inlet estuary. Platell & Potter (1996) argued that the preferred environment of *B. chilensis* is deep sandy sediment containing a high amount of shell debris. Since this habitat does not occur in Leschenault Inlet estuary, the absence of this species is perhaps not surprising. No such explanation can be given for the capitellid *H. filiformis*, which occurs in shallow-water sands of Wilson Inlet. Possibly, this species is replaced by *Mediomastus* sp in the Leschenault Inlet estuary.

There were three polychaete species recorded from the Leschenault Inlet estuary that, to our knowledge, have never been found in south-western Australian estuaries before: *Lumbrineris* cf *latreilli, Glycera* cf *americana,* and *Ampharetidae* sp This is likely due to sparse sampling in many earlier studies. Augener (1914) gives a description of an ampharetid, *Isolda warnbroensis* that bears some similarity to our specimens. However, it is likely that the species from Leschenault Inlet estuary is yet undescribed.

Three species previously recorded for the Leschenault Inlet estuary were not retrieved in our study. Anon (1983) listed *Eunereis* sp and Deeley (Murdoch University, *pers. comm.*) recorded *Boccardiella limnicola* and *Leitoscoloplos normalus* in 1991. The latter species were recorded from oligohaline regions of the estuary not sampled in this study. Furthermore, Anon (1983) records *Ceratonereis erythraeensis* as the dominant species of Leschenault Inlet estuary, constituting 9-15% of the total benthic fauna. We suggest that this species was really *C. aequisetis*. This possible mis-identification highlights the general problem of polychaete identification, particularly since there is no recent taxonomic work available on the polychaetes of south-western Australia.

Spatial patterns

Most of the fifteen polychaete species present in the Leschenault Inlet estuary may be regarded as euryhaline marine species. They are frequently recorded from marine sites and appear to be restricted by salinity within the estuary. This is reflected in the decreasing polychaete species diversity from lower to upper salinity fields. However, records of *C. aequisetis* are restricted to estuaries (Augener 1913; Hutchings & Murray 1984) so it appears to be able to withstand large changes in salinity.

Spatial distributions of particular species were linked to salinity, depth and substrate. Salinity appeared to affect the distributions of *N. gravieri*, *C.* cf *capitata* and *S. simplex* which showed a preference for the mid- to lower estuarine fields that is typical for euryhaline marine species within estuaries (Kennish 1990). *C. aequisetis* had a shallow depth preference (which may have been a function of temperature, oxygen or seagrass distribution) resulting in a depth-controlled, concentric distribution pattern within the estuary. Abundance of *C.* cf *capitata* showed some correlation with substrate; it had highest abundances in mud to muddy sand substrates. *C. capitata* is known to tolerate the low oxygen regime of muddy sapropel in seagrass swards (Remane & Schlieper 1971) which could account for its high abundance in the basinal muds of the Leschenault Inlet estuary. In contrast, *N. graveri* showed no clear substrate preference since it was common in substrates ranging from sandy intertidal to basinal mud.

Hutchings & Murray (1984) recorded detailed environmental parameters for species found in the Hawkesbury River and southern New South Wales estuaries. In general, their habitat remarks for particular species agree well with our distribution data, as discussed below. *C. aequisetis* was the most widespread estuarine species recorded in southern estuaries of New South Wales, which is consistent with distribution and abundance data for this species in Leschenault Inlet estuary. *C. capitata* was found in sandy muds with salinity greater than 30‰, which is corroborated by our records which restrict this species to the lower to mid-estuarine fields where salinity rarely drops to mesohaline values. Similarly, both Hutchings & Murray (1984) and this study recorded *S. simplex* most commonly from intertidal areas. Both studies found that species of the genera *Phyllodoce, Neanthes, Glycera, Diopatra* and *Lumbrineris* were restricted to muddy sands in salinity regimes comparable to marine environments. Finally, Hutchings & Murray (1984) found *A. ehlersi* restricted to sand and muddy sand in salinities ranging from 5-37‰, which is consistent with our records of this species from deltaic sands to mid-estuarine central basin mud.

Habitat associations

Wurm & Semeniuk (2000) recognised nineteen habitat types within the estuary, of which fourteen were sampled in this study. Maximum abundance of the main polychaete species with respect to this habitat classification is shown in Table 2.

C. aequisetis was most common in intertidal and shallow platform habitats, but showed no substrate preference. *N. gravieri* typically occurred in muddy basinal habitats in the lower to mid-estuarine fields. *C.* cf *capitata* was most abundant in the muddy sand to mud habitats in mid- to lower estuary. *S. simplex* was restricted to the lower to middle estuary, where it appeared to favour intertidal sand habitats (Table 2).

Site data on polychaete diversity and abundance indicate that the habitat framework correlates fairly well with polychaete distributions, since there are only minor differences in abundance between sites representing the same habitat. For example, *C. aequisetis* shows some differences between intertidal habitats in the Collie Delta region of Transect A (sites A1, A2 *vs* A6, A7) which could be attributed to factors such as food source, grain size preference

Table 2. Maximal abundance of species with respect to individual site within the habitat framework of Wurm & Semeniuk (2000).

Habitat (sites)	Site	*Ceratonereis aquisetis*	*Nephtys gravieri*	*Capitella* cf *capitata*	*Scoloplos simpex*
deltaic intertidal sand	1	***	*	-	*
	6	*	-	-	*
	7	**	*	-	*
deltaic sand	2	***	*	*	*
lower estuarine intertidal muddy sand	5	***	*	**	*
lower estuarine platform muddy sand	4	***	*	**	-
	9	**	*	***	*
	10	***	*	***	*
	13	-	-	-	-
lower estuarine platform sand	8	**	*	***	*
lower estuarine platform sandy mud	14	***	*	*	-
lower estuarine basinal sandy mud	3	-	***	**	*
lower estuarine basinal mud	11	-	*	**	*
	12	-	*	***	-
mid-estuarine intertidal sand	19	***	***	**	*
mid-estuarine platform sandy mud	18	*	*	*	*
mid-estuarine platform muddy sand	15	***	*	***	-
	16	*	-	***	-
mid-estuarine basinal mud	17	*	**	***	-
upper estuarine intertidal sandy mud	20	***	-	-	-
upper estuarine intertidalo mud	21	***	-	**	-
	22	***	*	**	-

Species are classified as: very common (***; typically >10 specimens per site); common (**; typically between 5-10 specimens per site); and uncommon (*; typically less than 5 specimens per site).

or aquatic vegetation. Differences in abundance of this species also occurred between sites C15 and C16 and between site B13 and other lower estuarine platform muddy sand habitats that may be attributed to differences in water depth. However, since polychaetes were never recorded from site B13 and only low numbers were collected from site B14, the differing numbers at these sites may have been related to disturbance caused by their vicinity to the effluent disposal pipeline. Since the habitats of the dominant polychaete species appear to be well defined, they can be used to define assemblages which characterise three different regions of the estuary.

1. Sediments in the deltaic region and the lower to mid-estuarine sections of the western platform margin characteristically had high numbers of *C. aequisetis*, with less common occurrences of other species including *C.* cf *capitata* and *N. gravieri*. We use this characteristic to define a *Ceratonereis-Capitella-Nephtys* assemblage found mainly in shallow-water sands with salinities ranging from 15-40‰.
2. Lower to mid-estuarine deep-water basinal mud was characterised by *C. cf capitata* and *N. gravieri*, with *C. aequisetis* being least abundant. Here, we delineate a *Capitella-Nephtys* assemblage for muds with salinities from 35-45‰.
3. The northern part of the estuary was largely dominated by *C. aequisetis*, with less common occurrences of *C. cf capitata*, defining a *Ceratonereis-Capitella* assemblage for shallow muds with salinities from 25-60‰.

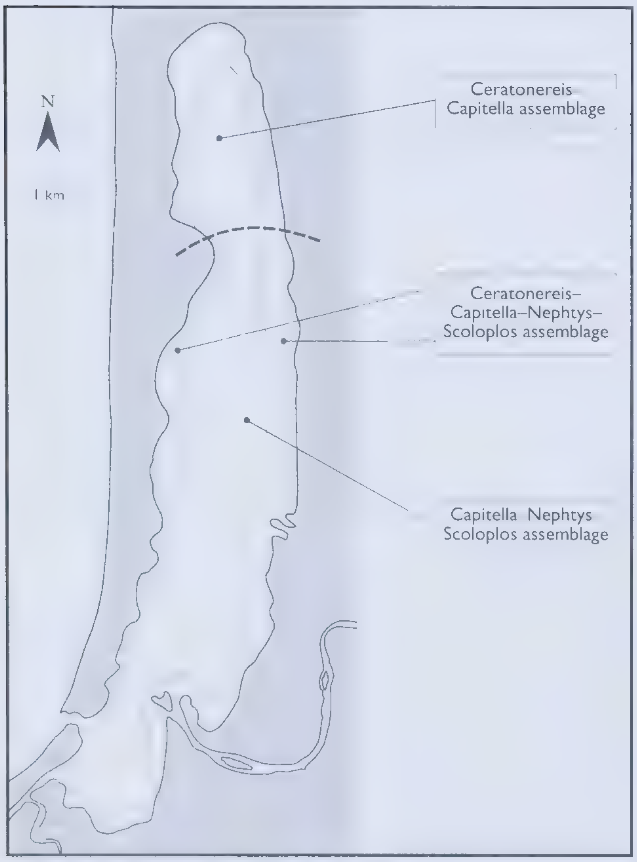


Figure 9: Polychaete assemblages for Leschenault Inlet estuary (linked to salinity, depth and substrate), based on habitat classification of Wurm & Semeniuk (2000).

We suggest that the habitat preferences of the three major polychaete species in Leschenault Inlet estuary (Figs 2, 3; Table 2) are sufficient to distinguish lower to mid-estuarine shallow- and deep-water assemblages and an upper estuarine assemblage. Figure 9 illustrates the expected spatial ranges of these assemblages, based on the habitat mapping by Wurm & Semeniuk (2000).

Temporal variation

Average seasonal abundance throughout the five-year period revealed that all three main species typically show unimodal circa-annual periodicity in population abundance (Fig. 5). Although average peak abundances were mostly recorded in February or May *i.e.* late summer to autumn, the exact timing of the peak varied from site to site. For example, *C. aequisetis* peaked in abundance in December at shallow upper estuarine sites D20 and D21, which were also the sites where highest abundances of this species occur (Fig. 5). This may indicate preferred recruitment of this species in shallow warm, muddy substrate of the upper estuary. However, since neither body size nor abundance of larvae was recorded, we can not strictly separate adult migration from juvenile recruitment in temporal patterns.

Kaleijta (1992) presented a detailed study of the population dynamics of *Ceratonereis keiskama* and *Ceratonereis erythraeensis* from a South African estuary. Maximum annual recruitment of *C. keiskama* occurred in December, whereas the recruitment timing of *C. erythraeensis* varied both between years and between sites. Our data suggest that the life cycle of *C. aequisetis* is similar to that of *C. erythraeensis*. Kaleijta (1992) also reported size-dependent stratification of young animals in superficial (<5 cm) and larger animals in deeper regions of the substrate (5-30 cm) for *C. erythraeensis*. A similar tendency in *C. aequisetis* would have caused under-sampling of adult specimens in this study due to shallow coring, particularly during winter.

Overall seasonal abundance changes for the whole population of polychaetes in Leschenault Inlet estuary appear to be highly unpredictable (Fig. 4). Given the rather stable circa-annual pattern of chemical and physical parameters such as temperature, salinity or oxygen content (Wurm & Semeniuk 2000), this result implies that the effect of seasonally varying abiotic factors can only be recognised on smaller spatial scales. In general, population dynamics at different sites were asynchronous (Fig. 5). Hence, locally determined amplitude and phase relationships of population dynamics masked any regular circa-annual periodicity in the average overall abundances of a given species. In addition, large variability in species abundance within a single year (Fig. 6) and from year to year (Fig. 7) limited detection of underlying dynamics.

Beukema *et al.* (1993) argued that variability of abundances could be interpreted as a genuine species characteristic. In their twenty-year record of benthic infauna of the Wadden Sea, coefficients of variation in year-to-year sampling were larger than 0.8 for *Nephtys* and *Nereis*, and even larger than 1.2 for *Harmothoë* and *Anaitides*. In our study, variability was similarly high and more importantly, lacked any obvious habitat dependency. Future studies on seasonal abundance will have to take into account that large numbers of samples are required to give a robust estimate of average abundance and that long-term monitoring is required to determine whether the observed temporal pattern is due to variability or due to other factors.

Finally, coincident anti-cyclic patterns at neighbouring sites indicate that, in spite of all the variability between sites, nearby populations may be subjected to the same environmental stresses and follow rather similar long-term abundance fluctuations (Fig. 8 *e.g.* August 1984 to August 1986). Such coherent phase shifts in the timing of peaks and troughs in abundance recorded at different sites did not necessarily relate to abiotic factors.

At some sites there appeared to be an anti-cyclic population pattern between two species (*e.g.* at A3, where *C. aequisetis* was most abundant when *N. Gravieri* is least abundant; Fig 6). In spite of such examples, there was no consistent proportional or inverse relationship between abundances of different species. The impact of predators on polychaete populations was not investigated in this study, and may also be a factor contributing to temporal variation on annual and longer time scales.

During the sampling period T A Semeniuk (2000) recognised a long-term decline in abundance of small benthic Crustacea, and Semeniuk & Wurm (2000) noted a similar long-term decline in numbers of some mollusc species. The data presented for the polychaetes in this paper supports this overall trend. However, the marked drop in crustacean numbers over the period 1984-1985 was not reflected in the polychaete abundance. Rather, at some sites, polychaetes were relatively more abundant during this period (see Fig. 8). Hence, benthic faunal groups show different sensitivity to environmental change, and would appear to have different potential as environmental indicators.

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Occurrence of *Amphipholis squamata* (Echinodermata: Ophiuroidea) in relation to habitat in the Leschenault Inlet estuary

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Abstract

The occurrence of a cosmopolitan ophiuroid echinoderm, *Amphipholis squamata* (Delle-Chiaje) in the Leschenault Inlet estuary of south-western Australia has been recorded at varying intervals over a period of 17 years (1982-1999). This occurrence is noteworthy because the ophiuroid is inhabiting an estuary whereas most other records of the species in Western Australia are oceanic, and because the biogeographic range of the species is extended. During 1982-1987, *A. squamata* generally had sporadic low density populations in the Leschenault Inlet estuary, in restricted habitats mostly in areas with mud to muddy-sand substrate, moderate detritus levels, usually some seagrass and/or algae present, at the boundary between the middle to upper estuarine salinity fields, well-oxygenated water, and water temperature range of *ca* 15-30 °C. However, during August 1984 and September 1986 to March 1987, and in October 1990, *A. squamata* populations were dense, mainly located at the boundary between the middle to upper estuary. Since 1990, the species appears to have returned to its sporadic low density and restricted occurrence.

Keywords: ophiuroid, *Amphipholis squamata*, Leschenault Inlet, estuary, south-western Australia.

Introduction

The brittle star, *Amphipholis squamata* (Delle-Chiaje 1828), is a cosmopolitan ophiuroid echinoderm found in marine coastal waters of both the northern hemisphere (north-eastern America, northern Europe, the Mediterranean and the northern Indo-Pacific) and the southern hemisphere (*circum* South Africa, New Zealand and Australia). Around Australian coastal waters, *A. squamata* has been recorded as far north as Beagle Gulf and Melville Bay, Northern Territory, to as far south as Tasmania (Rowe & Gates 1995). In Western Australian, the species has been recorded ranging from as far north as Rowley Shoals to the Albany region and southern coast (Marsh 1986, 1991). In its *circum*-Australian distribution, the species has been found in a number of habitats including coral reefs, algae-covered rock platforms, and areas with sandy or muddy substrates.

This paper records *A. squamata* in Leschenault Inlet estuary, near Bunbury, south-western Australia (33° 17' S, 115° 41' E). This occurrence is noteworthy, firstly because the ophiuroid is inhabiting an estuary, whereas the majority of other records of the species in Western Australia are oceanic, and secondly because the biogeographic range of the species in an estuarine setting is extended. *A. squamata* is described in terms of its general biology and the spatial and temporal variation in abundance and distribution of the species with respect to different habitat settings within the estuary. Habitat variables (*i.e.* geomorphology, substrate, vegetation, water depth, temperature, salinity and oxygen content) are examined to determine any association with patterns of abundance and distribution of the animal. The known ecology of ophiuroids is applied to the specific situation existing in Leschenault Inlet estuary for *A. squamata*.

Setting

Leschenault Inlet estuary is located on the coast of the southern Swan Coastal Plain, south-western Australia. The Inlet is shallow and elongate, with a central mud-floored basin (1.5-2.0 m deep), a system of bordering seagrass-vegetated, shallower water, sand and muddy sand platforms and ramps (generally < 1 m deep), and a northern shallow water mud-floored flat (Fig 1A). It is separated from the Indian Ocean by the Leschenault Peninsula barrier dunes, and to the east it is bordered by a high ridge of sand and limestone (Mandurah-Australind Ridge). To the south and south-east there are deltaic complexes at the mouth of the Collie and Preston Rivers. Wurm & Semeniuk (2000) subdivide the estuarine system into numerous habitat units and hydrochemical zones. Relevant information on the habitats, as they relate to the occurrence of ophiuroids in Leschenault Inlet estuary, are described in Table 1.

Methods

Estuarine benthic invertebrate faunal surveys were carried out at Leschenault Inlet estuary from 1982 to 1987 by the V & C Semeniuk Research Group during the period 1982-1987, and these are supplemented by observations and collections of Deeley (School of Environmental Science, Murdoch University, *pers. comm.* 1998) and Bastyan (Water & Rivers Commission, Denmark *pers. comm.* 1998), and collections by this author in September 1998 and May 1999. This author and Deeley sampled with cylindrical cores as described below and Bastyan opportunistically collected a sample of algae in a 6-dram container.

Twenty-two sampling sites were established along 4 east-west transects to study benthic fauna in Leschenault Inlet estuary (Fig 1B). These transects and sampling sites, together with the physical and chemical characteristics of the water body considered to be relevant to the benthic fauna (oxygen concentration, temperature and salinity), are described in Wurm & Semeniuk (2000). Sampling sites

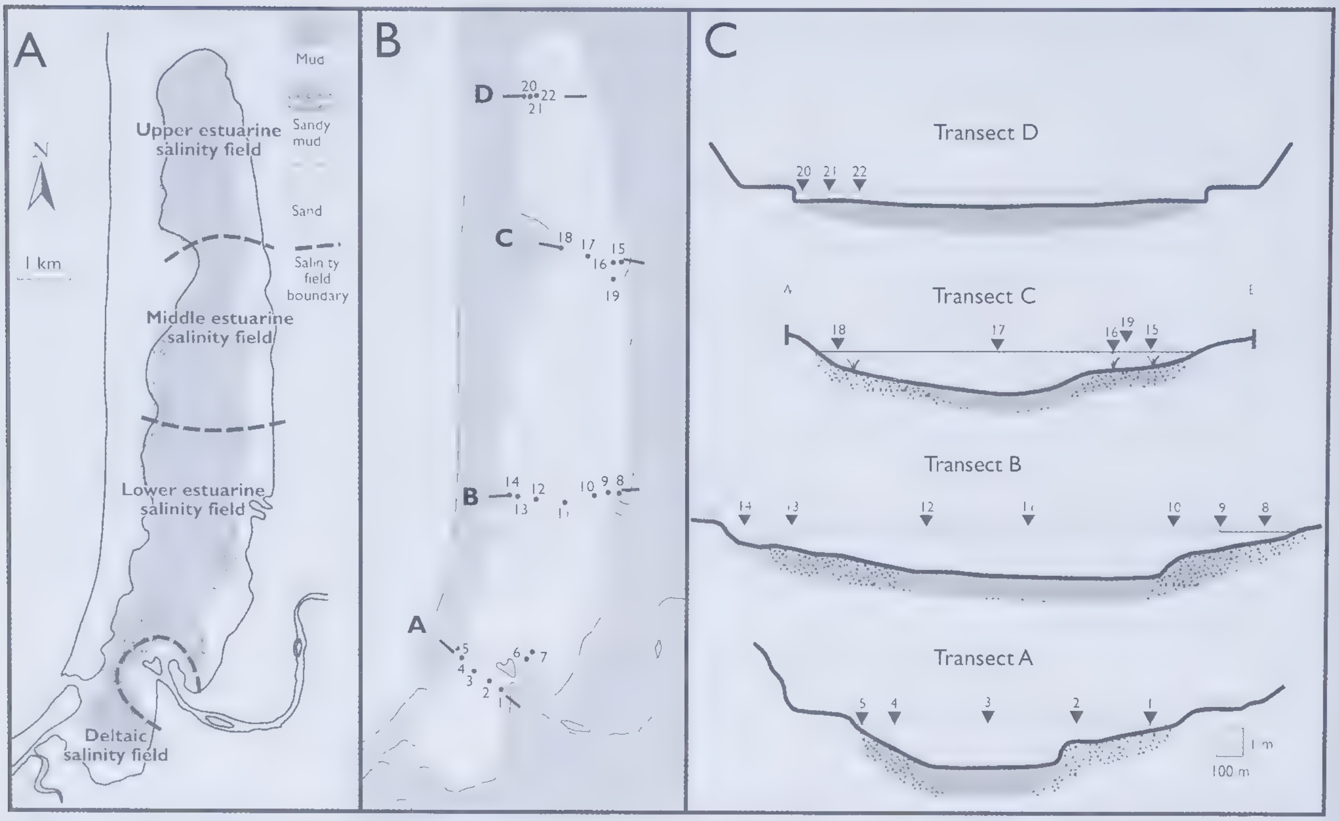

Figure 1. **A:** Generalised map of the habitats, showing location of platform and basin, substrate types, and salinity fields (after Wurm & Semeniuk 2000). **B:** Location of the Transects and the 22 sampling sites in the Leschenault Inlet estuary (after Wurm & Semeniuk 2000). **C:** Cross sections across estuary along the Transect C where the ophuroid was most abundant, showing bathymetry, substrate types and sampling sites.

within a framework of water depths and substrates are shown in Fig 1C.

At the various study sites along the transects, benthic biota were sampled within a 10 m diameter homogenous area, annually, quarterly, to monthly, depending on location. Ophiuroids were sampled using two sizes of cores; a 25 cm x 25 cm x 25 cm square box corer and a 10 cm diameter x 15 cm long cylindrical corer (Semeniuk T A 2000; Wurm & Semeniuk 2000). At each sampling site one box core sample was taken to determine numbers of ophiuroids in the substrate by counting on-site; the sample was washed through a 1 mm sieve, and after counting, ophiuroids were released back to the environment. Similarly, five randomly-placed replicate cylindrical cores were used to determine ophiuroid numbers, and take into account patchiness in distribution, but were collected and stored for counting and further study in the laboratory. These small cores were washed through a 1 mm sieve in the field, and the sieved residues were fixed in 10% formalin, and transported to the laboratory where the ophiuroids were separated from other biota and then preserved in 1 % phenoxitol. Ophiuroid specimens from these small cores were then counted and measured under a binocular microscope. Mean and standard deviation were calculated for the abundance figures of each sampling event.

Results

General biology

Over the five-year period 1982-1987, a total of 76 ophiuroid specimens were collected by small cores from Leschenault Inlet estuary. The specimens ranged in disc diameter from 0.5 mm (minimum) to 3.0 mm (maximum). The majority of specimens were adults with disc diameters equal to or greater than 2 mm and a maximum arm length of 10 mm. Twelve per cent of the specimens were juveniles with disc diameters of 1.0 mm or less. Mean disc diameter of all *A. squamata* collected in the study was 1.8 mm. There was minor evidence of autotomy with a small number of specimens showing re-growth of one or more arms. Only one specimen from site 17 showed current indications of brooding with enlarged bursae evident.

Distribution of *A. squamata* (1982-1987)

Out of the 22 sites sampled over five years between 1982 and 1987 in Leschenault Inlet estuary, *A. squamata* occurred mainly along Transect C, at sites 15, 16, 17 and 18 (Table 1; Fig 2.). Characteristics of those sites where the ophiuroid has been most abundant (*i.e.* a mean number > 10 per 625 cm^2, *viz* sites 4, 15, 16, 17 and 18) have been summarised in Table 1 in terms of depth, substrates, seagrass cover, detritus content of the sediment, salinity, oxygen, and temperature.

Abundance over space and time (1982-1987)

Distribution of *A. squamata* varied spatially, with the larger population of ophiuroids in the relatively shallow water eastern and western platform and central basin deep water mud habitats at sites 15, 16, 17 and 18 (Figs 2, 3 & 4). However, the occurrence of *A. squamata* was temporally and spatially sporadic. *A. squamata* was not collected during every sample period and when present was not always found in every replicate sample. Moreover, apart from one occurrence at site 17 in August 1984, no specimens were recorded at any of the sampling sites for a relatively lengthy period from November 1983 to August 1986.

Over the sampling period of 1982-1987, there were relative peaks in population densities in May 1983, August 1983, August 1984, and between September 1986 and March 1987. The most dense populations were at sites 15, 16, 17, and 18, though site 4 had a relatively dense population in February 1987. Even when the species was present fairly consistently in time, its abundance still varied during the year, with most ophiuroids present during spring through summer to autumn.

Occurrence in 1982-1987

Opportunistic sampling in 1990/91, 1995, 1998, and 1999 showed that *A. squamata* was present in the estuary beyond the 1982-1987 sampling period, sometimes in sites other than those which the ophiuroids most commonly inhabited (Fig 4).

During the sampling by the V & C Semeniuk Research Group in 1982-1987, as part of systematic survey of estuarine benthos in the estuary, 22 sites along Transects A, B, C and D were sampled. Ophiuroids were present mostly at sites 15, 16, 17, 18 along Transect C, in shallow water seagrass-vegetated habitat, and seagrass-free deeper water, and additionally they were recorded at site A4 near "The Cut". Bastyan carried out systematic sampling over the whole inlet along numerous transects, in October 1990 as part of a widespread survey of aquatic vegetation of Leschenault Inlet estuary (Hill *et al.* 2000). During this survey ophiuroids were extremely abundant (hundreds of ophiuroids per square decimeter) along Transect C and over northern subtidal basin. *A. squamata* was epibiotic on dense mats of algae present at that time. A sample of algae with over 600 ophiuroid individuals in a 6-dram container was lodged with WA Museum. Bastyan again carried out systematic sampling over the whole inlet, for aquatic vegetation in April 1991, and found little evidence of ophiuroids. In 1995 Deeley sampled 5 sites located widely over the whole estuary and found that the ophiuroids occurred only at two sites, near C17 (6 individuals)and near the centre of Transect B (5 individuals). In September 1998 this author resampled site C16. No ophiuroids were noted from five 25 cm x 25 cm box cores. In May 1999 this author resampled sites A4, B9, B11, B13, C16, C17, C18. Only one ophiuroid individual was recorded at site C16 from 5 replicate box cores and 5 replicate small 10 cm cores.

Table 1. Description of the main sites where *A. squamata* occurred (data from Wurm & Semeniuk 2000).

Characteristic of the habitat	**Site 4:Western seagrass vegetated shallow water platform**	**Sites 15 & 16:Eastern seagrass vegetated shallow water platform**	**Site 17:Central basin, seagrass-free**	**Site 18:Western seagrass vegetated shallow water platform**
depth	average water depth of 50 cm	average water depth of 50 cm	average water depth of 130 cm	average water depth of 50 cm
substrate	muddy sand	muddy sand	mud	sandy mud
seagrass and algae	continuous seagrass meadows: dominantly *Halophila ovalis* and *Gracilaria* species	low seagrass meadows: dominantly *Halophila ovalis* and some *Ruppia maritima;* algae: an unidentified *Phaeophyta* species, *Chaetomorpha* species (Chlorophyta) and to a minor extent *Gracilaria* species (Rhodophyta)	none	continuous seagrass meadows: dominantly *Halophila ovalis,* and algae
detritus in sediment	225 gm dry wgt/m^2	40-50 gm dry wgt/m^2	*ca* 10 gm dry wgt/m^2	70 gm dry wgt/m^2
salinity field	lower estuarine salinity field: mean salinity close to sea water, with a small standard deviation (winter: 32.0 ‰, summer: 43.5 ‰)	middle salinity field: mean salinity value higher than sea water and with a large standard deviation (winter: 29.5 ‰, summer: 48.5 ‰)	middle salinity field: mean salinity value higher than sea water and with a large standard deviation (winter: 29.5 ‰, summer: 48.0 ‰)	middle salinity field: mean salinity value higher than sea water and with a large standard deviation (winter: 30.0 ‰, summer: 46.0 ‰)
oxygen concentration	< 5 mg L^{-1}	< 5 mg L^{-1}	< 5 mg L^{-1}	< 5 mg L^{-1}
water temperature range	*ca* 15 °C in winter to *ca* 30 °C in summer	*ca* 15 °C in winter to *ca* 30 °C in summer	*ca* 15 °C in winter to *ca* 25 °C in summer	*ca* 15° C in winter to *ca* 30° C in summer

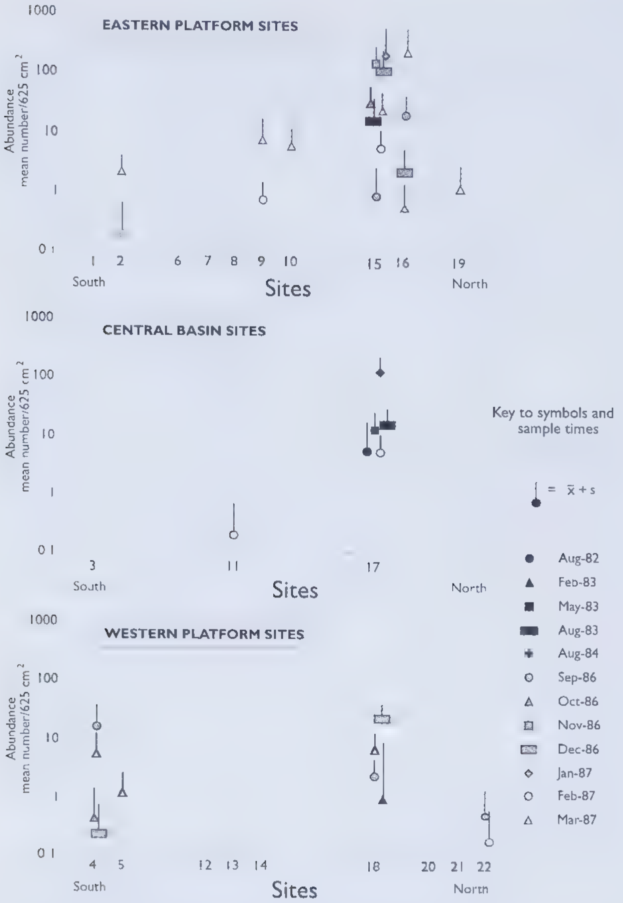

Figure 2. Mean abundance and positive standard deviation of the ophiuroid within each of the main habitat settings (*viz* eastern platform central basin, western basin) for the various sampling times (see Fig 1 for site locations). Table 2 notes which sites were sampled annually, quarterly, or monthly.

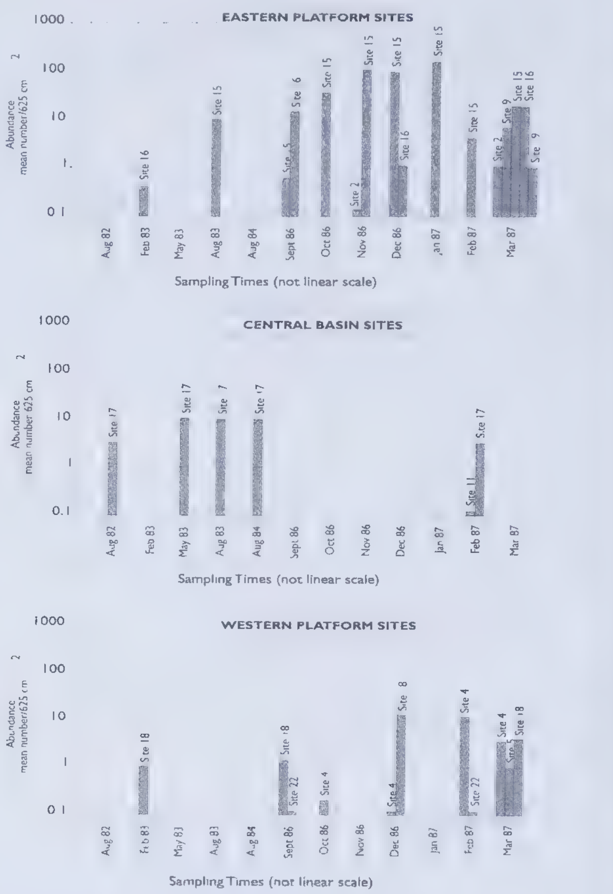

Figure 3. Histogram showing mean abundances only of the ophiuroid at individual sites within main habitat settings, with respect to sampling times (see Fig 1 for site locations).

Discussion

Leschenault Inlet estuary presents an interesting environment for explaining the abundance and distribution of *A. squamata* with respect to habitat preferences encompassing biotic factors such as breeding strategy and mechanisms of dispersal, and abiotic factors such as substrate types, salinity, water temperature, water depth and water oxygen content. *A. squamata* is a globally-distributed species, adapted to the variable physical conditions of intertidal zones, and able to tolerate a range of environmental parameters (Emson & Foote 1980). Consequently, it is an opportunistic ophiuroid most likely to be able to survive under the estuarine conditions present in Leschenault Inlet estuary. In size, the specimens collected from Leschenault Inlet estuary were comparable with the marine Albany specimens collected by Marsh (1991) suggesting that normal growth expression was not limited by environmental conditions in the estuarine habitats.

In relation to the abundance of the animal, between 1982 and 1999, the occurrences may be summarised as follows;

1. from 1982-1986, *A. squamata* had sporadic low-level populations in the Leschenault Inlet estuary, in habitats mostly located along Transect C, the zone where the upper estuarine field adjoins the middle estuarine field;
2. in September 1986 to March 1987, *A. squamata* populations were dense, with the main populations again centred on Transect C, but with others along Transects A and D;
3. in October 1990, the ophiuroid was recorded as extremely abundant on vegetation along Transect C and in shallow water to the north; and
4. since 1990, the species appears to have returned to its sporadic low level occurrence, again in habitats mostly located along Transect C.

A range of heterogeneous habitats occurs in the Leschenault Inlet estuary, and *A. squamata* has populated a restricted number of them, *viz* the muddy sand seagrass-vegetated eastern and western shallow water platforms located in the mid-estuarine salinity field and the muddy vegetation-free central deep water basin. Comparisons of some key habitat features of the most populated sites and their implication to ophiuroid survival in Leschenault Inlet estuary are shown in Table 3 below.

A. squamata is a hermaphroditic viviparous species, not subject to the cyclic population variations reflecting larval recruitment, and consequently Hendler (1991) suggests that

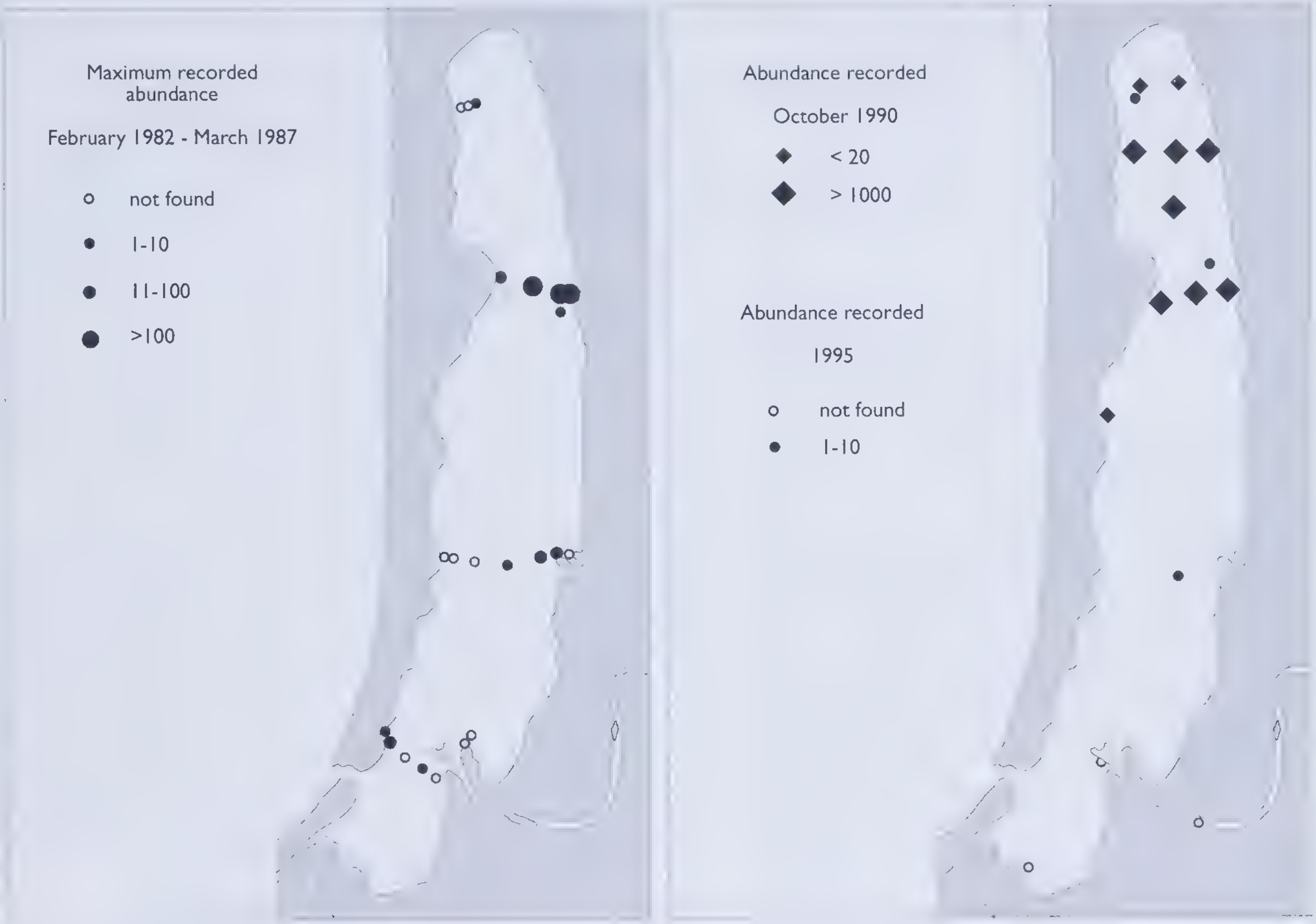

Figure 4. Occurrence of the *A. squamata* during the 1982-1987 sampling period, in 1990, and in 1995. Note that only positive occurrence results were shown for the 1990 information, even though the whole area of the estuary was systematically sampled.

brooding development of more than one cohort simultaneously may result in patchy recruitment and limited distribution. The ophiuroid may also migrate into environments by a mechanism termed "rafting dispersal", where the animal attaches to floating weed, a characteristic of some brooding ophiuroid taxa (Fell 1953). During the time of maximum abundance in October 1990, the ophiuroids were attached to local drifting bottom weed (Bastyan, Water & Rivers Commission, Denmark, *pers. comm.*) indicating that rafting dispersal may have been operating. Another method of dispersal which has been noted for ophiuroids is epizoism *e.g. Ophiocnemis marmorata* can "hitch-hike" on rhizostome jellyfish (Marsh 1998). It is possible that *A. squamata* may also occasionally adopt this method of dispersal. These latter mechanisms of dispersal may result in ophiuroids bypassing many possible suitable habitats before coming to reside in their final habitat. Thus, ophiuroid populations in Leschenault Inlet estuary could be maintained by two mechanisms; intra-estuarine maintenance (*i.e.* bursal brooding), and extra-estuarine rafting or hitch-hiking.

However, once established as a population within the estuary, the persistence of the ophiuroids would be determined by salinity (freshwater influences on local hypersalinity, and regions of stable near-oceanic salinity), hence they appear to contract to the region around Transect C. Once established as a population in the middle-upper estuarine region, the species may also maintain its populations over a number of favourable seasons by intra-estuarine reproduction.

Wide fluctuations in the abundance of ophiuroid populations in Leschenault Inlet estuary ranged from short duration population peaks (numbering in the thousands in October 1990) to virtual absence, even in its preferred habitats, for lengthy periods (*e.g.* mainly between November 1983 and August 1986). The temperature fluctuations described by Wurm & Semeniuk (2000) and the salinity record of Leschenault Inlet estuary over the period November 1983 to August 1986 show no apparent departure from the seasonal fluctuations evident for 1982-1987, indicating that temperature or salinity change probably did not eliminate the species from the estuary. The reasons for changes in abundance of the ophiuroids in Leschenault Inlet estuary over time is therefore unknown.

Overall, *A. squamata* occurs in Leschenault Inlet estuary as an opportunistic colonizing species which inhabits the more marine-like habitats consisting of shallow water muddy substrates, moderate to warm temperatures and less fluctuating, euhaline salinity found towards the northern end of the estuary. While in general the abundance and distribution of the ophiuroid was low and limited respectively (with the exception of occasional population explosions), *A. squamata* seems to be a persistent species within the Leschenault Inlet estuary. However, its mode of recruitment, either externally from marine sources via rafting/hitch-hiking, or internally from intra-estuarine populations, or a combination of both modes is worth further study.

Table 3. Comparisons of key habitat features of sites 15, 16, 17 and 18 in Leschenault Inlet estuary and their implications.

Habitat attribute	Sites 15, 16 & 18	Site 17	Implications
depth	50 cm	130 cm	globally, the species ranges from intertidal to continental slope (500 m) habitats, but in Leschenault Inlet estuary it inhabits essentially shallow water habitats
sediment type	muddy sand	mud	mud and muddy sand are the preferred substrates in Leschenault Inlet estuary: these are sediment types (amongst others) that Cherbonnier & Guille (1978), ascribe to A. squamata
seagrass	seagrass cover	seagrass-free	in situ macrophytes are not a determinant
oxygen	water column well oxygenated	water column well oxygenated	A. squamata possesses a high tolerance for low oxygen levels as a corollary of burrowing in anoxic sediments, thus oxygen is not a limiting factor
detritus	moderate to high content	low content	detritus content is not a determinant
freshwaterinfluences	not freshwater influenced	not freshwater influenced	freshwater potentially eliminated the species in the middle to southern parts of the estuary, where it is generally absent
marine water influences (proximity to the oceanic source)	marine derived, stable salinity	marine derived, stable salinity	ophiuroids reach their maximum abundance at sites distal from the oceanic source, where salinity fields are stable; they are uncommon both in hypersaline fields along Transect D, and deltaic fields along Transect A, implicating salinity as a determinant
temperature	ca 15 °C in winter to ca 30 °C in summer	ca 15 °C in winter to ca 25 °C in summer	temperature does not appear to be a determinant in Leschenault Inlet estuary

Acknowledgments: Most of the samples collected between 1982 and 1987 were provided by the V & C Semeniuk Research Group, as part of a study into the estuarine environment of the Leschenault Inlet. Monthly data between 1986 and 1987 were obtained by P A S Wurm as part of an Honours project on molluscs undertaken at Murdoch University, and lodged with samples held by V & C Semeniuk Research Group as part of the estuarine studies mentioned above. Abundance data for 1990 and 1995 were provided by G Bastyan and D Deeley; this is gratefully acknowledged. L Marsh provided identifications, taxonomic assistance, and relevant literature; this help is also gratefully acknowledged. The manuscript was critically read by V Semeniuk.

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The fish fauna and finfish fishery of the Leschenault Estuary in south-western Australia

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Abstract

This paper collates unpublished and published data on the fish faunas of the large basin and Collie River regions of the Leschenault Estuary in 1982/83 and 1993/94, and provides information on the commercial and recreational fisheries in that estuary. The most abundant of the 42 fish species recorded in eight six-weekly samples collected from the nearshore, shallow waters of the basin in 1994, were the long-finned goby *Favonigobius lateralis*, the sandy sprat *Hyperlophus vittatus* and the atherinids *Leptatherina presbyteroides* and *Atherinosoma elongata*; these four species collectively contributing 83.0% to the total number of fish caught. Of the 42 species, 20 were marine species which use the estuary as a nursery area (marine estuarine-opportunists), while 13 complete their life cycles in the estuary, of which seven are also represented by marine populations. The contribution made to the total number of individuals by marine estuarine-opportunists and marine stragglers collectively (32.1%) was far lower than that of species which complete their life cycles in the estuary (67.9%). The presence in shallow waters of large numbers of representatives of species that spawn in the estuary, which parallels the situation found in other south-western Australian estuaries, is probably related to the maintenance of stable conditions and high salinities during late spring and summer when these species, which generally have marine affinities, typically spawn. The composition of the fish fauna of the shallows of Leschenault Estuary differs markedly from that of comparable waters in Koombana Bay into which this estuary discharges. Indeed, the most abundant species in the bay, the flathead sandfish *Lesueurina platycephala*, which contributed *ca* 25% to the total numbers in those marine waters, was never recorded in the estuary. The fish catches in offshore, deeper waters of the estuary basin and Collie River comprised larger species and, unlike the situation in shallow waters, were dominated by marine estuarine-opportunists and the semi-anadromous Perth herring *Nematalosa vlaminghi*. However, the composition of the fish fauna in offshore, deeper waters of the basin differed markedly from that in corresponding waters in the Collie River. This was mainly due to the presence in the basin of far more species and relatively greater numbers of species, such as yellow-eye mullet (*Aldrichetta forsteri*), tailor (*Pomatomus saltatrix*) and Australian herring (*Arripis georgiana*), and to the occurrence in the river of relatively greater numbers of Perth herring and sea mullet (*Mugil cephalus*). Length-frequency data provide strong evidence that, within the estuary, the small species *F. lateralis, L. presbyteroides* and *A. elongata* spawn mainly in summer and typically have a one year life cycle. The small juveniles of the marine species *A. forsteri* and *M. cephalus* are recruited into the estuary between mid- or late autumn and early spring, which is consistent with the fact that the spawning period of these two species is very protracted, extending through autumn and winter. Both of these mugilids were represented in some months by three or more age classes. Recruitment into the estuary of King George whiting (*Sillaginodes punctata*) occurs in spring, while that of yellow-finned whiting (*Sillago schomburgkii*) and prickly toadfish (*Contusus brevicaudus*) takes place in summer and autumn, respectively. This reflects spawning occurring in winter and early spring in the case of the first species and in summer with the second and third species. These three species were apparently represented mainly by only two age classes. While length-frequency data show that *P. saltatrix* also uses the estuary as a nursery area, the modal size classes did not follow such consistent trends throughout the year, possibly reflecting a recruitment, in some years, of the 0+ age class of both the spring and autumn-spawning cohorts. The growth of all of these species essentially ceased during the cold winter months. The feeding mode of each of the most abundant species can be allocated to one of the following categories. (1) herbivores which feed mainly on the algae associated with seagrass, *e.g. Hyporhamphus melanochir, Pelates sexlineatus*. (2) detritivores, *e.g. M. cephalus, N. vlaminghi*. (3) omnivores which feed on algae and a range of invertebrates, *e.g. A. forsteri, Amniataba caudavittata*. (4) lower-order carnivores which feed on small benthic invertebrates, *e.g. A. elongata, F. lateralis, L. presbyteroides, S. punctata, S. schomburgkii, Torquigener pleurogramma*. (5) higher-order carnivores whose prey includes larger and more active invertebrates and fish, *e.g. Argyrosomus japonicus, P. saltatrix*. The former commercial fishers in Leschenault Estuary, who were restricted to fishing in the basin, shifted from gill nets to haul nets in recent years to reduce the amount of bycatch. *Aldrichetta forsteri, M. cephalus, S. schomburgkii* and *S. punctatia* were the main commercial fish species, contributing 55.5, 20.2, 11.1 and 6.6%, respectively, to the total wet weight of all fish species caught between 1981 and 1997. The recreational fishery is dominated by three species of whiting (*S. punctata, S. schomburgkii* and *Sillago burrus)* and tailor *P. saltatrix*.

Keywords: Leschenault Estuary, shallow and deep waters, fish species, size compositions, use of the estuary, recruitment, diets, commercial and recreational fisheries.

Introduction

The estuaries of temperate south-western Australia typically contain a large central basin region, which is fed by tributary rivers, the downstream regions of which are saline. The basin region opens to the sea via a narrow and usually short entrance channel (Hodgkin & Lenanton 1981). Some of these estuaries, *e.g.* the Swan River, Peel Harvey, Leschenault and Nornalup Walpole estuaries, remain permanently open, whereas others such as the Wellstead Estuary and Wilson Inlet become closed, either seasonally or for longer periods through the formation of sand bars at their mouths (Lenanton & Hodgkin 1985). However, the Peel Harvey Estuary used to become closed in some years in the past, but is now kept permanently open through dredging (Bradby 1997). Another category of estuary is provided by that of the Moore River, which does not contain a large central basin and opens intermittently during the year when, as a result of input from artesian springs and/or increased rainfall, the volume of water becomes sufficiently great to breach the bar at its mouth (Young *et al.* 1997). In the case of these south-western Australian estuaries, the narrowness and shallowness of their entrance channels and the large areas occupied by their basins (Lenanton & Hodgkin 1985; Potter *et al.* 1990), together with the presence of a small tidal range in the region (Hodgkin & di Lollo 1958), mean that tidal water movement within their middle and upper reaches is far less pronounced than it is, for example, in the numerous macrotidal estuaries found in temperate regions of the northern hemisphere (*cf* Spencer 1956; Kennish 1986; Stephens & Imberger 1996).

During the last 20-25 years, detailed studies have been carried out on the ichthyofaunas of several estuaries in south-western Australia (see review by Potter & Hyndes 1999). These studies, which employed various techniques to sample different water depths within these estuaries throughout the year, have elucidated the ways in which the compositions of the fish faunas and numbers of the main fish species in the different regions of these estuaries change seasonally and in relation to environmental conditions (*e.g.* Chubb *et al.* 1981; Loneragan *et al.* 1986, 1989; Potter *et al.* 1983, 1988, 1993; Potter & Hyndes 1994; Valesini *et al.* 1997; Young *et al.* 1997). The studies on ichthyofaunal compositions in the different estuaries have been accompanied by studies of the biology of the more numerous fish species in these estuaries, which have helped clarify the ways in which each of those species use estuaries (*e.g.* Chubb *et al.* 1981; Prince & Potter 1983; Chrystal *et al.* 1985; Potter *et al.* 1988; Hyndes *et al.* 1992; Laurenson *et al.* 1993a). The results of each of the various studies have been considered collectively to ascertain the main features of the ichthyofaunas of estuaries in south-western Australia in general and the way in which the particular characteristics of the ichthyofaunas vary according to both the type and location of the estuary, *e.g.* open *vs* closed and lower west coast *vs* south coast respectively (Potter & Hyndes 1999).

A number of marine fish species, such as the sea mullet *Mugil cephalus* and the yellow-eye mullet *Aldrichetta forsteri*, use the permanently-open estuaries on the lower west coast of Australia as nursery areas (*e.g.* Chubb *et al.* 1981; Lenanton *et al.* 1984), thereby paralleling the situation with several marine fish species in estuaries in temperate regions of the northern hemisphere (*e.g.* Haedrich 1983; Claridge *et al.* 1986; Elliott & Dewailly 1996). However, the prevalence of the 0+ age class of these and other marine species tends to be far lower in estuaries on the south coast of Western Australia, a feature that apparently reflects in part a greater distance of these estuaries from the main spawning grounds of those species (Potter & Hyndes 1994). Although those marine fish species, which use estuaries regularly and typically as nursery areas, are sometimes referred to as estuarine-dependent in other regions (Blaber *et al.* 1989; Elliott *et al.* 1990; Kennish 1990; Whitfield 1998), such species in south-western Australia almost invariably also employ as nursery areas those sheltered marine waters that are found, for example, in coastal embayments (Lenanton & Potter 1987). We thus regard the term marine estuarine-opportunist as more applicable for these species in south-western Australia. While the larvae of a few marine estuarine-opportunist species are transported into the lower regions of estuaries in south-western Australia, the larvae of such species are absent or occur in relatively low numbers in the main body (basins) of these estuaries (Neira *et al.* 1992; Neira & Potter 1992a,b, 1994). This contrasts with the situation found in macrotidal estuaries in the temperate regions of the northern hemisphere, where the larvae of certain comparable species capitalise on the strong tidal water movements to enter and then move through those estuaries by using tidal and/or passive transport (Fortier & Leggett 1982; Norcross & Shaw 1984; Boehlert & Mundy 1988). The movement of marine estuarine-opportunists into and through the estuaries of south-western Australia typically occurs at the juvenile stage and is presumably achieved largely through swimming in an upstream direction. The use of the term marine estuarine-opportunist for the above group of species enables such species to be distinguished from the marine stragglers, which occur irregularly and usually in low numbers in estuaries and generally in the regions of high salinity near the estuary mouth.

Although only a few fish species are adapted to completing their life cycles in estuaries, some of these species, such as certain hardyheads (atherinids) and gobies, are particularly abundant in south-western Australian estuaries, which presumably reflects the influence of one or more of the following features. First, the small input of freshwater discharge from tributary rivers in late spring and summer, when rainfall is minimal, combined with a small tidal action, leads at that time to salinities remaining high and stable in these estuaries and to water movement being largely brought about by wind action and changes in barometric pressure. Such stable conditions thus approximate to those in sheltered nearshore, marine waters outside the estuary, which act as the habitat for several small marine fish species (Ayvazian & Hyndes 1995) and are thus ideal for spawning by species with a marine origin. It is also important to recognise that, during the periodic landlocking to which many estuaries in south-western Australia have been subjected, there would have been strong selection pressures, particularly amongst short-lived species, to favour those individuals of any species that could spawn within the estuary. This would help account for the fact that some of the fish species that complete their life cycle in estuaries, such as the cobbler *Cnidoglanis macrocephalus* and the gobbleguts *Apogon rueppellii*, are also represented by genetically-discrete populations in coastal waters (Watts 1991; Ayvazian *et al.* 1994).

The only truly diadromous species in south-western Australia, which therefore requires an estuary to act as a migratory route between the marine and freshwater environments in which it spends different periods of its life cycle, is the pouched lamprey *Geotria australis*. This anadromous species spawns in freshwater and feeds parasitically on fish at sea (Potter *et al.* 1986). However, for convenience, the Perth herring *Nematalosa vlaminghi*, which spends a period feeding at sea but later migrates into its spawning grounds in the upper and reduced salinity areas of estuaries (Chubb & Potter 1984), is referred to as semi-anadromous. The few freshwater fish species that are found in estuaries are usually confined to the upper and brackish reaches of those estuaries (Loneragan *et al.* 1989).

This study has collated published and unpublished data on the fish fauna of the basin and saline, riverine reaches of the Leschenault Estuary and also of Koombana Bay into which that estuary discharges (Anon 1983; Potter *et al.* 1997; Tiivel *et al.*, Murdoch University, unpublished data). These data are then used to demonstrate the ways in which the compositions of the fish faunas in the shallow waters of an estuary can differ markedly from those in shallow, sheltered coastal waters just outside that estuary. The composition of the fish faunas in offshore, deeper waters of both the basin and riverine regions of the estuary, which are likely to contain larger fish than the shallows, have also been determined and compared to ascertain whether certain species are relatively more abundant in one or the other of these two very different environments. Length-frequency data for several of the most abundant species have been analysed in order to determine the times of recruitment, size compositions, probable age compositions and patterns of growth of those species. Data are also provided on the diets of several of the most abundant species. The ichthyofaunal composition and biology of the main fish species in Leschenault Estuary have been compared with those of other south-western Australian estuaries to help place in perspective the role played by that estuary in the life cycle of the main fish species found in that system. The policy of Fisheries Western Australia to buy out the licenses of commercial fishers, through a fisheries adjustment scheme, has now produced a situation whereby all fishers formerly licensed to operate in the Leschenault Estuary no longer have commercial access to this estuary. Nevertheless, catch data for this fishery have been analysed to elucidate the main species that formed the basis of this fishery and how the catches of these species have varied over the years. Preliminary data are also provided on the species composition of the recreational fishery.

Materials and Methods

Sampling regime in 1993/94

Sites in shallow waters of the basin of the Leschenault Estuary and Koombana Bay (Fig 1) were sampled during the day and night at six-weekly intervals between November 1993 and December 1994, using a 21.5 m long and 1.5 m high seine net (Table 1, see also Potter *et al.* 1997). This net contained two 10 m long wings, each with 6 m of 9 mm mesh and 4 m of 3 mm mesh, the latter leading into a 1.5 m wide bunt which likewise consisted of 3 mm mesh. The net swept an approximately circular area of 116 m^2 from the shoreline. Sampling was also carried out twice in the spring of 1993 and once in each of the ensuing summer, autumn and winter months using a 41.5 m long and 1.5 m high seine net during the day. This second seine net, which consisted of two 20 m long wings of 25 mm mesh and a 1.5 m bunt of 9 mm mesh, swept an area of 274 m^2. Although the lower and middle regions of the basin of Leschenault Estuary could be sampled by the 21.5 m seine net on each sampling occasion, this was not always possible in the upper estuary because the waters in that region sometimes declined to less than the 1.5 m height of this net. Emphasis has thus been placed on the results obtained for shallow waters in the lower and middle regions of the basin. Values for the salinities and water temperatures in the shallows of the basin of Leschenault Estuary and along the shoreline of Koombana Bay are given in Potter *et al.* (1997).

The fish faunas in deeper and more offshore waters at

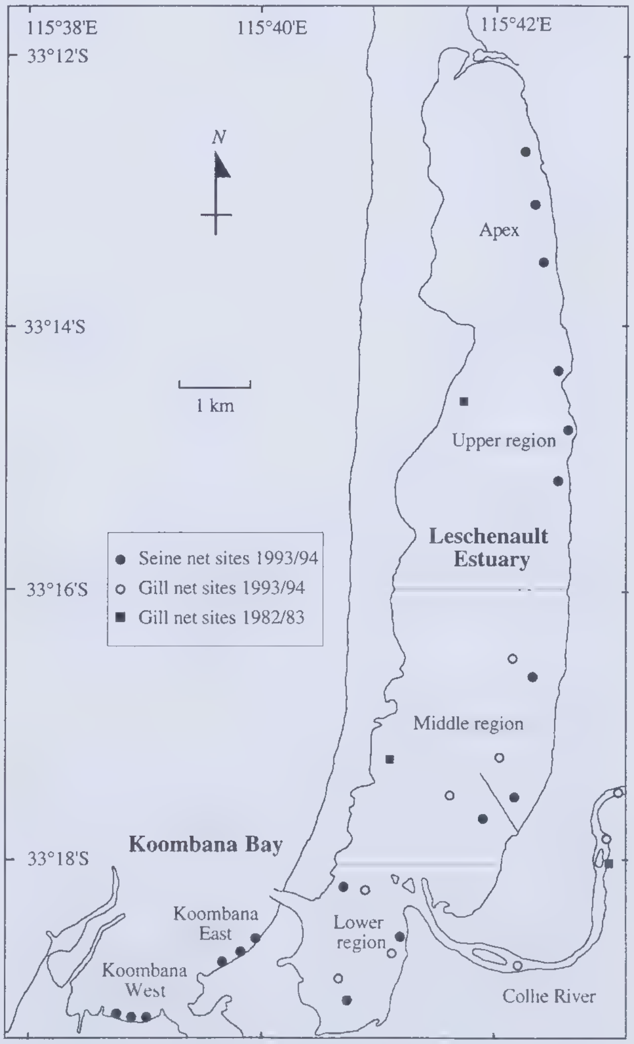

Figure 1. Map of Leschenault Estuary and Koombana Bay, showing the location of the sites sampled using the 21.5 and 41.5 m seine nets and the 120 m long sunken composite gill nets in 1993/94, and employing the 220 m long sunken and floating composite gill nets in 1982/83.

Table 1. Summary of sampling regimes used in the basin and Collie River regions of the Leschenault Estuary in 1993/94 and 1982/83. Numbers in parentheses provide data on the sampling regime in the river on those occasions when it differed from that in the basin. N.B. The rivers were not sampled by seine net in 1993/94. The six shallow water sites in Koombana Bay were sampled using the 21.5 m seine net on the same occasions as the shallow water sites were sampled with the same net in the basin of Leschenault Estuary.

	1993/1994			1982/1983	
	Seine net	Seine net	Gill net (sunken)	Seine net	Gill net (sunken and floating)
Net length	21.5 m	41.5 m	120 m (6 x 20 m panels)	103 m	2 x 220 m (11 x 20 m panels)
Mesh size	3 mm in bunt	9 mm in bunt	38-102 mm	9 mm in bunt	38-100 mm
Area swept (m^2)	116	274		1600	
Number of sites	6	6	6 (3)	10 (5)	2 (1)
Months sampled	Nov 93; Feb, Mar, May, Jun, Jul, Sep, Nov and Dec 94	Sep and Nov 93; Feb, May and Jul 94	Sep and Nov 93; Feb, May and Jul 94	May, Aug and Nov 82; Feb 83	May, Aug and Nov 82; Feb 83

six sites in the basin and at three sites in the saline region of the Collie River of the Leschenault Estuary were sampled using sunken, composite gill nets in each season between the spring of 1993 and winter of 1994, including twice in the first of those seasons (Table 1, Fig 1). The gill nets, which were 120 m long and comprised six 20 m long panels with sequential stretched mesh sizes of 38, 51, 63, 76, 89 and 102 mm, were set immediately prior to dusk and retrieved three hours later.

Sampling regime in 1982/83

The fish faunas of the basin and Collie River regions of the Leschenault Estuary were sampled in May, August and November of 1982 and in February of 1983 using seine and gill nets (Table 1). The seine net, which was 103 m long and 1.5 m high, consisted of two 50 m long wings of 25 mm mesh and a 3 m bunt of 9 mm mesh. Since the lower reaches of the Collie River contain steep banks and could thus not be sampled effectively using seine nets, the use of such nets had to be restricted to regions of this river that were > 4 km above the point that the river discharged into the basin. The net was pulled in a semicircle from the bank, covering in this case an area of 1 600 m^2. The data derived from seine netting at several sites in four seasons in 1982/83 have been used solely for the construction of length-frequency histograms. The composite gill net was 220 m long and consisted of eleven 20 m long panels, with each panel containing a different mesh size, *i.e.* 38, 44, 50, 56, 63, 69, 75, 81, 88, 94 and 100 mm. Two such gill nets were set at dusk for three hours at each site, one being weighted so that it sunk and rested on the estuary floor, while the other was buoyed so that it was suspended from the water surface. In each season, gill netting was undertaken at two sites in the basin and at one site in the river (Table 1, Fig 1).

The methods and dates of sampling in 1993/94 and 1982/83 are summarised in Table 1. The number of each fish species and the total length (to the nearest 1 mm) of each fish caught by the seine and gill nets on each occasion in the two periods were recorded, except when the sample of a species was large, in which case lengths of a random subsample of at least 100 representatives of each species were recorded. The number of each species caught by the 21.5 m seine net has been expressed as a density, *i.e.* number of fish per 100 m^2.

Length-frequency data

Since modes in the length-frequency data, recorded for each of the main larger fish species caught by seine and gill nets in 1993/94 and 1982/83, followed similar monthly trends, the length data collected for those species using both methods in the corresponding months in the two periods have been pooled. However, it should be recognised that, in those months when gill nets were not used, the cohorts of the large representatives of some fish species were not well represented.

Life cycle categories

On the basis of extensive studies of the biology of fish species in south-western Australian estuaries, each fish species collected in Leschenault Estuary and Koombana Bay has been allocated to one of the following life cycle categories, as defined in the introduction, namely marine straggler (S), marine estuarine-opportunist (O), semi-anadromous (SA), those that are found only in estuaries (E) and finally those that can complete the whole of their life cycle in either estuarine or marine environments (E&M). Although the hairy pipefish *Urocampus carinirostris* is abundant in sheltered marine habitats in eastern Australia (Howard & Koehn 1985; Steffe *et al.* 1989), it has never been found in this type of environment in south-western Australia. Thus, in south-western Australia, where this species does occur in estuaries, it is now regarded as estuarine rather than as both estuarine and marine as in Potter *et al.* (1997). While the sea garfish *Hyporhamphus melanochir* spawns in estuaries on the south coast of Western Australia (Neira & Potter 1992a, 1994), it almost certainly spawns only in marine environments on the lower west coast of this state, this difference between regions thus paralleling that of the blue-spotted flathead *Platycephalus speculator* (Hyndes *et al.* 1992). Those marine species that were caught in Koombana Bay, and yet have never been recorded in estuaries in south-western Australia, are referred to as solely marine (SM). Although the southern shovelnose ray *Aptychotrema vincentiana* was recorded in the shallows of Koombana Bay, but not in those of Leschenault Estuary (Potter *et al.* 1997), it has now been recorded in offshore, deeper waters of the basin of this estuary and is thus now considered to be a marine straggler rather than a solely marine species. The percentage contributions of each of the above different life cycle categories, both in terms of number of species and number of individuals, were determined for the shallows of both the lower and middle regions of the basin of Leschenault Estuary and of the western and eastern regions of Koombana Bay, using data derived from samples collected by the 21.5 m seine net at approximately six-weekly intervals in 1994.

Comparison of ichthyofaunal compositions

The mean densities of each fish species in the shallows of the lower and middle basins of Leschenault Estuary and in the western and eastern regions of Koombana Bay during the day and night, which were based on data derived from the catches obtained with the 21.5 m seine net in 1994, were standardised and root transformed and then subjected to classification and ordination using the PRIMER package (Clarke & Warwick 1994). Analyses of similarities (ANOSIM, Clarke 1993) was used to test whether the compositions of the fish faunas differed significantly among the above four regions and between day and night. The catch of each species per 3 hours by gill net in the basin and Collie River regions of Leschenault Estuary were likewise standardised and root transformed and subjected to analysis by classification and ordination. ANOSIM was employed to test whether the ichthyofaunal compositions in the two regions were significantly different.

Commercial and recreational fisheries

Data on the commercial fishery, *i.e.* the total number of boats fishing, the fishing effort (number of days spent fishing using gill and haul nets), and the wet weight of the total catch and of each of the main commercial finfish species in Leschenault Estuary in each year between 1981 and 1997, were extracted from the Fisheries Western Australia Catch and Effort Statistics (CAES). Data on the recreational fishery (Fisheries Western Australia) represent preliminary results of a creel census carried out in Leschenault Estuary during 1998.

Results and Discussion

Ichthyofauna of nearshore, shallow waters

Seine netting carried out at three sites in shallow waters of both the lower and middle regions of the basin of Leschenault Estuary, and at three sites in both the western and eastern regions of Koombana Bay, on eight occasions at six-weekly intervals throughout 1994, yielded 21 192 and 1 770 fish, respectively. After the number of fish caught in each sample had been adjusted to a constant area of 100 m^2 and been summed, the total number of fish recorded for the estuary and bay were 18 269 and 1 527, respectively (Table 2). The number of fish caught in shallow waters was thus approximately twelve times greater in the estuary than in the bay. Analysis of variance demonstrated that the mean overall densities of fish were significantly greater ($P < 0.001$) in the estuary basin than in the bay (Potter *et al.* 1997). Forty two and 34 species were recorded in the estuary and bay, respectively (Table 2). The number of species in shallow waters was significantly greater in both the lower and middle region of the basin than in the eastern region of Koombana Bay, but not in its western region which is more protected (Potter *et al.* 1997).

The most abundant species in the shallow waters of Leschenault Estuary, *i.e.* those contributing > 10% to the total numbers of fish, were the gobiid *Favonigobius lateralis*, the clupeid *Hyperlophus vittatus* and the atherinids *Leptatherina presbyteroides* and *Atherinosoma elongata* (Table 2). The mugilids *Aldrichetta forsteri* and *Mugil cephalus*, the apogonid *Apogon rueppellii*, the sillaginid *Sillaginodes punctata*, the gobiids *Pseudogobius olorum* and *Afurcagobius suppositus* and the atherinid *Leptatherina wallacei* each contributed between 0.8 and 2.8%. The Gobiidae, Atherinidae and Clupeidae were the most abundant families, contributing 37.2, 28.3 and 22.5% to the total numbers of fish, respectively, and thus collectively 88% (Table 3). The Mugilidae, Sillaginidae and Apogonidae were the next most abundant families, contributing 3.6, 2.6 and 2.2%, respectively.

Favonigobius lateralis and *Aldrichetta forsteri* were the only two of the ten most abundant species in the estuary which also ranked amongst the 13 most abundant species in Koombana Bay (Table 2). *Favonigobius lateralis* ranked fifth in the bay and *A. forsteri* second. The most abundant species in shallow waters of the bay was the leptoscopid *Lesueurina platycephala*, which was never caught in the estuary. The third and fourth most abundant species in the bay were the sillaginid *Sillago bassensis*, which was only very occasionally caught in the estuary, and the tetraodontid *Contusus brevicaudus*, which was moderately abundant in the estuary (Table 2).

In terms of number of individuals, the most abundant family in shallow waters of Koombana Bay was the Leptoscopidae, which was represented by a single species and contributed *ca* 25% to the total numbers. The next three most numerous families in the bay by far were the Sillaginidae (18.1%), Mugilidae (16.7%) and Tetraodontidae (15.3%), each of which ranked amongst the seven most abundant families in Leschenault Estuary (Table 3).

Twenty of the 42 fish species caught in the basin of Leschenault Estuary use that estuary regularly and in appreciable numbers as a nursery area (Table 4). The most abundant of these marine estuarine-opportunist species were the sandy sprat *Hyperlophus vittatus*, the mullets *Aldrichetta forsteri* and *Mugil cephalus* and the King George whiting *Sillaginodes punctata* (Table 2). However, approximately 97% of the *H. vittatus* were caught in November 1994 and were represented in that month exclusively by young 0+ fish. Surprisingly, only nine species of marine straggler were recorded in the estuary basin (Table 4), which is far fewer than the numbers of this category found in other estuaries on the lower west coast (see Potter & Hyndes 1999). Thirteen of the fish species caught in the basin complete their life cycle within the estuary and, of these, seven are also represented by marine populations (Table 4).

Table 2. Life cycle categories (SM = solely marine, S = marine straggler, O = marine estuarine-opportunist, E&M = estuarine and marine, E = estuarine), length range, number (N), percentage contribution (%) and ranking by abundance (R) of each species of elasmobranch and teleost caught in the shallows of the lower and middle regions of the Leschenault Estuary and western and eastern regions of Koombana Bay using the 21.5 m seine net between February and December 1994. In this and Tables 3 and 4, the number of each fish species represents the total for all samples, after the number in each sample had been adjusted to a constant density, *i.e.* number of fish per 100 m^2.

Species	**Life cycle category**	**Length range (mm)**	**Estuary**			**Bay**		
			N	**%**	**R**	**N**	**%**	**R**
Favonigobius lateralis	E&M	8-76	6196	33.9	1	124	8.1	5
Hyperlophus vittatus	O	21-57	4109	22.5	2	12	0.8	12
Leptatherina presbyteroides	E&M	11-67	3025	16.6	3	4	0.3	21
Atherinosoma elongata	E	12-87	1840	10.1	4			
Aldrichetta forsteri	O	23-295	509	2.8	5	254	16.7	2
Apogon rueppellii	E&M	15-73	385	2.1	6			
Sillaginodes punctata	O	23-236	374	2.0	7			
Pseudogobius olorum	E	18-60	367	2.0	8			
Leptatherina wallacei	E	21-64	297	1.6	9			
Afurcagobius suppositus	E	15-69	215	1.2	10			
Mugil cephalus	O	23-149	144	0.8	11	2	0.1	26
Gymnapistes marmoratus	O	15-93	107	0.6	12	7	0.5	15
Torquigener pleurogramma	O	81-154	93	0.5	13	6	0.4	16
Contusus brevicaudus	O	22-130	85	0.5	14	228	14.9	4
Sillago burrus	O	18-99	83	0.5	15	11	0.7	14
Haletta semifasciata	S	20-155	75	0.4	16			
Stigmatophora argus	S	51-137	68	0.4	17			
Pelates sexlineatus	O	13-201	67	0.4	18	15	1.0	11
Arripis georgiana	O	41-209	26	0.1	19	48	3.1	7
Urocampus carinirostris	E	39-91	22	0.1	20			
Amoya bifrenatus	E&M	22-129	20	0.1	21			
Siphamia cephalotes	E&M	20-51	18	0.1	22			
Hyporhamphus melanochir	O	66-231	17	0.1	23	6	0.4	16
Scobinichthys granulatus	S	32-73	16	0.1	24	1	<0.1	31
Rhabdosargus sarba	O	16-220	15	0.1	25	2	0.1	26
Atherinomorus ogilbyi	O	46-152	14	0.1	26	51	3.3	6
Gerres subfasciatus	O	12-155	12	0.1	27	2	0.1	26
Enoplosus armatus	S	23-41	10	0.1	28			
Sillago schomburgkii	O	82-256	9	<0.1	29	31	2.0	8
Gonorynchus greyi	O	82-167	8	<0.1	30	2	0.1	26
Sillago bassensis	S	28-183	7	<0.1	31	235	15.4	3
Engraulis australis	E&M	60-76	6	<0.1	32	3	0.2	22
Callogobius mucosus	O	57-96	5	<0.1	33			
Pseudorhombus jenynsii	O	55-263	5	<0.1	33	1	<0.1	31
Ammotretis elongatus	S	23-163	4	<0.1	35	31	2.0	8
Spratelloides robustus	S	24-53	4	<0.1	35	3	0.2	22
Cnidoglanis macrocephalus	E&M	37-445	3	<0.1	37	6	0.4	16
Pomatomus saltatrix	O	32-291	3	<0.1	37	6	0.4	16
Amniataba caudavittata	E	41-163	3	<0.1	37			
Platycephalus speculator	O	79-299	1	<0.1	40	6	0.4	16
Pseudolabrus parilus	S	22	1	<0.1	40			
Cristiceps australis	S	129	1	<0.1	40			
Trygonorhina fasciata	SM	227				1	<0.1	31
Aptychotrema vincentiana	SM	400				1	<0.1	31
Pelsartia humeralis	SM	78-161				29	1.9	10
Arripis truttaceus	O	36-210				3	0.2	22
Lesueurina platycephala	SM	19-101				379	24.8	1
Cynoglossus maculipinnis	SM	82-157				3	0.2	22
Paraplagusia unicolor	SM	32-125				12	0.8	12
Scorpis aequipinnis	S	35-54				2	0.1	26
Total number of species				42			34	
Total number of fish				18269			1527	

Table 3. Number (N), percentage contribution (%) and ranking by abundance (R) of each family of elasmobranch and teleost caught in the shallows of Leschenault Estuary and Koombana Bay using the 21.5 m seine net between February and December 1994.

Families	Leschenault Estuary			Koombana Bay		
	N	%	R	N	%	R
Gobiidae	6803	37.2	1	124	8.1	6
Atherinidae	5176	28.3	2	55	3.6	7
Clupeidae	4113	22.5	3	15	1.0	11
Mugilidae	653	3.6	4	256	16.7	3
Sillaginidae	473	2.6	5	277	18.1	2
Apogonidae	403	2.2	6			
Tetraodontidae	178	1.0	7	234	15.3	4
Scorpaenidae	107	0.6	8	7	0.5	13
Syngnathidae	90	0.5	9			
Odacidae	75	0.4	10			
Terapontidae	70	0.4	11	44	2.9	9
Arripidae	26	0.1	12	51	3.3	8
Hemiramphidae	17	0.1	13	6	0.4	14
Monacanthidae	16	0.1	14	1	0.1	24
Sparidae	15	0.1	15	2	0.1	19
Gerreidae	12	0.1	16	2	0.1	19
Enoplosidae	10	0.1	17			
Gonorynchidae	8	<0.1	18	2	0.1	19
Engraulididae	6	<0.1	19	3	0.2	18
Bothidae	5	<0.1	20	1	0.1	24
Pleuronectidae	4	<0.1	21	31	2.0	10
Plotosidae	3	<0.1	22	6	0.4	14
Pomatomidae	3	<0.1	22	6	0.4	14
Platycephalidae	1	<0.1	24	6	0.4	14
Clinidae	1	<0.1	24	152	10.0	5
Labridae	1	<0.1	24			
Leptoscopidae				379	24.8	1
Cynoglossidae				15	1.0	11
Rhinobatidae				2	0.1	19
Scorpididae				2	0.1	19
Total number of families		**26**			**25**	
Total number of fish		**18269**			**1527**	

Table 4. Number (N) and percentage contribution (%) of species and individuals to each life cycle category collected in the nearshore, shallow waters of Leschenault Estuary and Koombana Bay using the 21.5 m seine net between February and December 1994.

Life cycle category	Estuary		Bay	
	N	%	N	%
Species				
Solely marine	0	0	6	17.6
Marine straggler	9	21.4	5	14.7
Marine estuarine -opportunist	20	47.6	19	55.9
Estuarine & marine	7	16.7	4	11.8
Estuarine	6	14.3	0	0
Total	**42**		**34**	
Individuals				
Solely marine	0	0	425	27.8
Marine straggler	187	1.0	272	17.8
Marine estuarine -opportunist	5684	31.1	693	45.4
Estuarine & marine	9653	52.8	137	9.0
Estuarine	2745	15.0	0	0
Total	**18269**		**1527**	

The number of individuals belonging to species which complete their life cycles within the estuary represented *ca* 68% of the total number of fish caught in the estuary (Table 4). Within this category, the numbers of those species, which are also represented by marine populations, contributed *ca* 53% to the total number of fish, while those that are found exclusively in estuaries contributed 15% (Table 4). The total percentage contribution made by species that complete their life cycles in the estuary is far greater than in the large Swan River and Peel Harvey estuaries to the north, but far less than those in Wilson Inlet and the Nornalup-Walpole Estuary on the south coast (Potter & Hyndes 1999).

The fish caught in nearshore, shallow waters of Koombana Bay contained six species that were never recorded in the estuary and five that only occasionally strayed into the estuary (Table 4). These 11 species collectively accounted for over 45% of the total number of fish caught in the bay. Eighteen of the 20 species of marine estuarine-opportunists found in Leschenault Estuary were also collected in Koombana Bay (Tables 2, 4). The individuals in this life cycle category contributed *ca* 45% to the total number of fish caught in the bay, emphasising that protected marine embayments, such as Koombana Bay, act as alternate nursery habitats to those provided by estuaries. The numbers of individuals of the remaining four species in Koombana Bay, which are represented by both estuarine and marine populations, contributed less than 10% to the total number of fish caught in that embayment (Table 4).

Classification of the mean densities of each species in nearshore, shallow waters during the day and night in 1994, based on data derived from samples collected using the 21.5 m seine net, separated all of the samples from the Leschenault Estuary from all of those from Koombana Bay (Fig 2). There was no tendency for the samples collected during the day and night in either the estuary or the bay to form separate clusters and neither was there any tendency for the samples in the two regions of the estuary to cluster separately. However, the majority of the samples from the western end of Koombana Bay did form a cluster that was discrete from all but two of the samples from the eastern and more exposed region of that bay (Fig 2).

MDS ordination of the same density data separated the samples from Leschenault Estuary from those in Koombana Bay (Fig 3 A). Furthermore, and likewise paralleling the results of classification, the samples from the two estuarine regions were interspersed on the ordination plot (Fig 3 B), whereas those from the two regions in Koombana Bay were relatively discrete (Fig 3 C) and shown by ANOSIM to be significantly different. *Lesueurina platycephala* was far more abundant in the eastern than western regions of the bay, whereas the reverse was true for *Sillago bassensis* and *Aldrichetta forsteri*. As with classification, no differences were found between the compositions of the samples collected during the day and night in either the estuary or the bay.

The pronounced difference between the compositions of the ichthyofaunas of nearshore, shallow waters of Leschenault Estuary and Koombana Bay parallel those recorded between comparable waters in the Blackwood River Estuary and Flinders Bay outside that estuary (Valesini *et al.* 1997). Although part of the reason for the difference between these two regions is the fact that some species are restricted to the estuary, it is also important to recognise

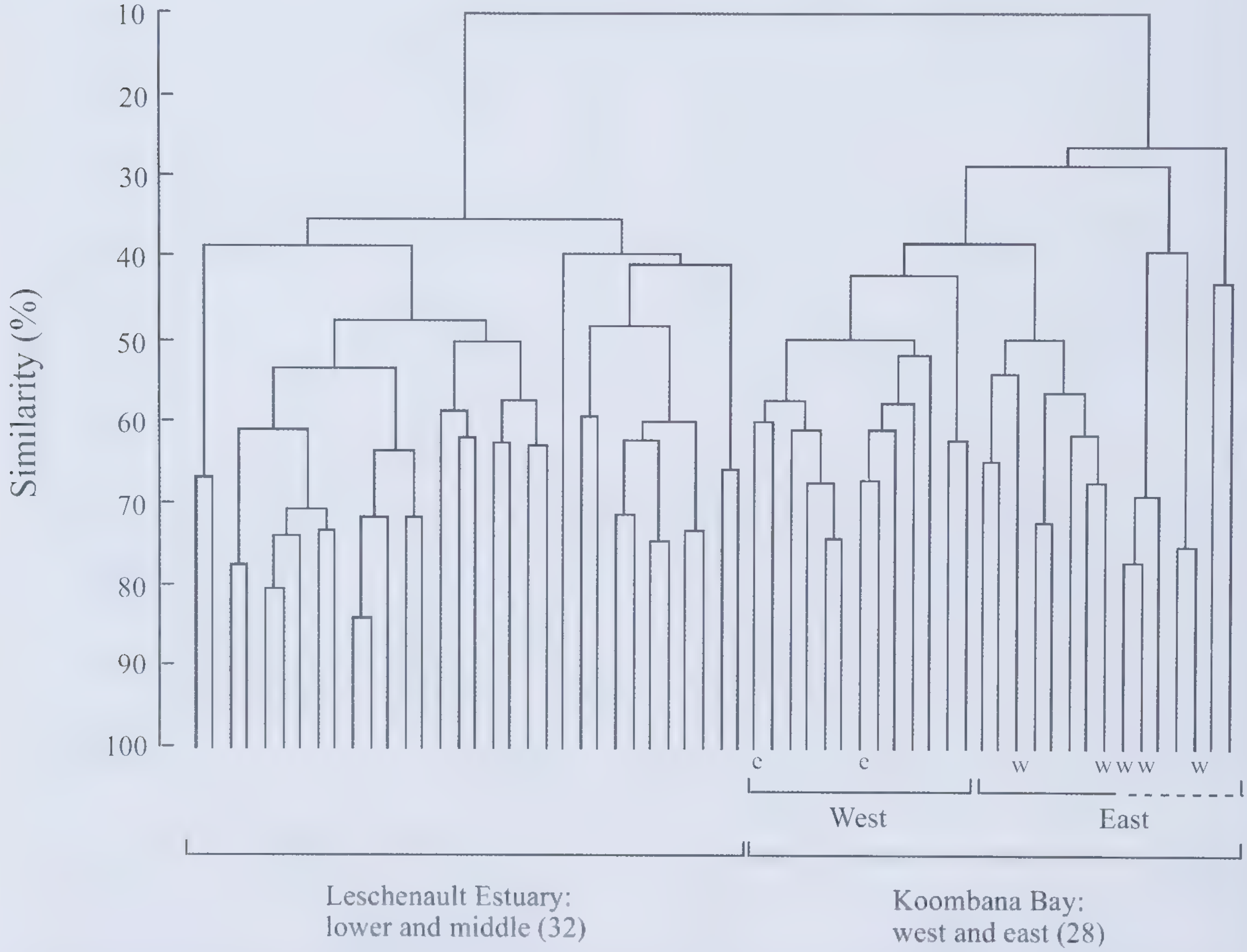

Figure 2. Classification of the mean densities of each fish species during the day and night in nearshore, shallow waters at three sites in both the lower and middle regions of the basin of Leschenault Estuary and at three sites in both the western and eastern regions of Koombana Bay. Here and in Fig 3, the data on densities were derived from samples collected with the 21.5 m seine net at approximately six-weekly intervals between February and December 1994. Numbers in parentheses represent number of samples. The samples from the western and eastern regions of Koombana Bay that fell within the clusters of predominantly the eastern and western regions, respectively, are designated as w and e, respectively. Modified from Potter *et al.* (1997).

that the juveniles of some species, such as *Mugil cephalus*, apparently have a strong preference for estuaries as nursery areas (Lenanton & Potter 1987).

Ichthyofauna of offshore, deeper waters

The total number of fish caught by gill netting seasonally in the basin and riverine regions of Leschenault Estuary in 1993/94, *i.e.* 1 518, was similar to that for those regions in 1982/83, *i.e.* 1 551, when the total amount of effort was similar (Table 1). The total numbers of fish caught in the basin and in the river during those two periods collectively were 1 146 and 1 923 respectively (Table 5). The most abundant species in the basin, *i.e.* the yellow-eye mullet *Aldrichetta forsteri*, contributed 26.9% to the total catch in that region, whereas in the river it ranked fourth and contributed only 2.8% to the total number of fish. The Perth herring *Nematalosa vlaminghi* was the second most abundant species in the basin, where it contributed 18.2%, and was the most numerous species in the river, where it comprised nearly 70% of the total catch (Table 5).

The only other species that contributed more than 10% in the basin was the tailor *Pomatomus saltatrix* with 12.2%, this species also ranking third in the river with a contribution of 3.6%. The sea mullet *Mugil cephalus* was the second most abundant species in the river, where it comprised nearly 20% of the total number of fish, which was far higher than the 3.3% it contributed in the basin. The marked tendency for juvenile *Mugil cephalus* to migrate into the Collie River and thus into waters of reduced salinity parallels the situation recorded for this species in other south-western Australian estuaries (*e.g.* Chubb *et al.* 1981; Potter & Hyndes 1994) and in estuaries elsewhere (*e.g.* Thomson 1957a). The four species of elasmobranch caught in the basin were all collected when salinities were high. One of these species, the eagle ray *Myliobatis australis*, is also often abundant in high salinity regions of the Nornalup-Walpole Estuary (Potter & Hyndes 1994). The three families that contributed most to the total number of fish in offshore, deeper waters of the Collie River, *i.e.* Mugilidae, Clupeidae and Pomatomidae, were the same as in deeper waters in the basin (Table 6). The representatives of no other family contributed over 10% to the total catch in deeper waters of either the river or basin.

Virtually all of the marine species caught by gill netting in deeper waters of the estuary basin and the Collie River were marine estuarine-opportunists (Table 7). The number of individuals of species representing this life cycle category contributed 77.4 and 29.1%, respectively, to those of all fish caught in these two regions. Only four of the species caught by gill net completed their life cycles in the estuary, namely the cobbler *Cnidoglanis macrocephalus*, the Australian anchovy *Engraulis australis*, the black bream *Acanthopagrus butcheri* and the yellowtail trumpeter *Amniataba caudavittata*. Moreover, these four species collectively contributed only 2.5% to the total number of fish caught throughout the estuary (Table 5). In contrast, the semi-anadromous category, represented solely by *N. vlaminghi*, contributed nearly 70% to the total catch in the river and 18.2% in the basin.

The number of species that complete their life cycle in the estuary, and their contribution to the total number of fish present, was far lower in offshore, deeper waters than in nearshore, shallow waters (*cf* Tables 4 and 7). This difference reflects the fact that many species belonging to this category are small and essentially confined to the shallows. However, there can be little doubt that, at least *Acanthopagrus butcheri*, which grows to a moderately large size and is relatively abundant in the deeper waters of the river, typically remains for the whole of its life cycle in its natal estuary (Chaplin *et al.* 1998).

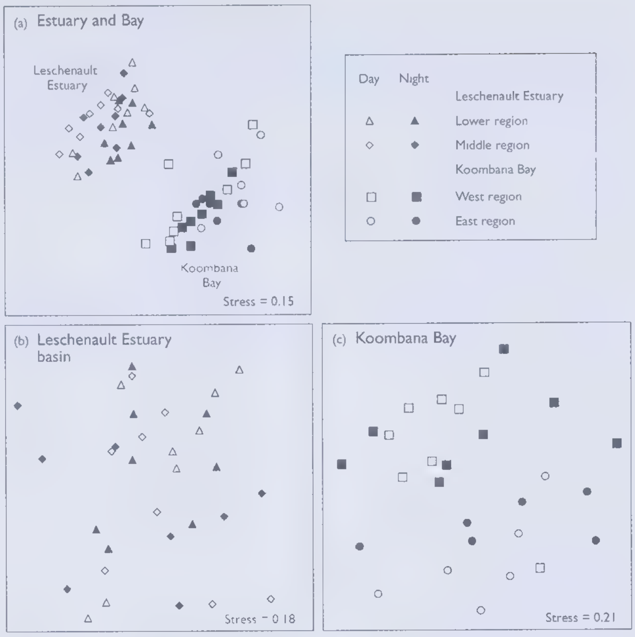

Figure 3. A: MDS ordination of the mean densities in 1994 of each fish species during both the day and night in nearshore, shallow waters of three sites in both the lower and middle regions of the basin of Leschenault Estuary and at three sites in both the western and eastern regions of Koombana Bay. **B** and **C** show separate ordination plots for the samples from the basin and bay, respectively. Modified from Potter *et al.* (1997).

Ordination separated the vast majority of the samples from deeper waters of the lower and middle regions of the estuary basin from those in the Collie River (Fig 4), thereby paralleling the results of the classification (not shown). ANOSIM showed that this difference was significant at $P < 0.05$.

Size composition of abundant species

In September 1993, the lengths of the long-finned goby *Favonigobius lateralis* produced a modal class at 45-54 mm (Fig 5). The modal length classes of the corresponding cohort in November 1993 and February 1994 were 40-49 and 40-44 mm, respectively. While this cohort was still represented by fish with a modal length class of 40-44 mm in March, a cohort of smaller fish with a modal length class of 20-24 mm appeared in this month, which clearly represented the new 0+ recruits. The modal length class of the 0+ fish increased to 25-29 mm in May and remained at this size interval during the ensuing late autumn to early spring months, but by November 1994 had increased to 30-34 mm. The strength of the 0+ age class and the accompanying decline in the numbers of the cohort of larger and presumably 1+ fish during the late autumn and winter months strongly indicate that *F. lateralis* typically has a one year life cycle in

Table 5. Life cycle categories (S = marine straggler, O = marine estuarine-opportunist, E&M = estuarine and marine, E = estuarine, SA = semi-anadromous), length range, number (N), percentage contribution (%) and ranking by abundance (R) of each species of elasmobranch and teleost caught using gill nets in offshore, deeper waters of the Leschenault Estuary basin and Collie River and for both of those regions combined, based on data collected in September 1993 to July 1994 and May 1982 to February 1983.

Species	**Life cycle category**	**Length range (mm)**	**Basin**			**River**			**Basin & River**		
			N	**%**	**R**	**N**	**%**	**R**	**N**	**%**	**R**
Aldrichetta forsteri	O	133-324	308	26.9	1	53	2.8	4	361	11.8	3
Nematalosa vlaminghi	SA	104-340	208	18.2	2	1325	68.9	1	1533	50.0	1
Pomatomus saltatrix	O	94-359	140	12.2	3	69	3.6	3	209	6.8	4
Sillago schomburgkii	O	174-282	90	7.9	4	5	0.3	9	95	3.1	5
Arripis georgianus	O	167-274	75	6.5	5				75	2.4	6
Pseudocaranx dentex	O	68-298	60	5.2	6				60	2.0	7
Pelates sexlineatus	O	135-197	50	4.4	7				50	1.6	8
Mugil cephalus	O	158-474	38	3.3	8	379	19.7	2	417	13.6	2
Arripis truttaceus	O	145-250	32	2.8	9				32	1.0	10
Myliobatis australis	O	497-1600	32	2.8	9				32	1.0	10
Cnidoglanis macrocephalus	E&M	310-500	27	2.4	11				27	0.9	12
Torquigener pleurogramma	O	111-131	15	1.3	12				15	0.5	16
Engraulis australis	E&M	91-129	14	1.2	13	8	0.4	8	22	0.7	15
Argyrosomus japonicus	O	210-520	13	1.1	14	32	1.7	5	45	1.5	9
Rhabdosargus sarba	O	110-130	9	0.8	15				9	0.3	17
Hyphorhamphus melanochir	O	170-390	8	0.7	16				8	0.3	18
Sillaginodes punctata	O	186-283	8	0.7	16				8	0.3	18
Gerres subfasciatus	O	116-184	5	0.4	18	18	0.9	7	23	0.7	14
Contusus brevicaudus	O	80-249	3	0.3	19	1	<0.1	12	4	0.1	20
Dasyatis thetidis	S	1600-2500	3	0.3	19				3	<0.1	21
Platycephalus laevigatus	S	125	2	0.2	21				2	<0.1	24
Aptychotrema vincentiana	S	700-801	2	0.2	21				2	<0.1	24
Mustelus antarcticus	S	440	1	<0.1	23				1	<0.1	26
Pseudorhombyus jenynsii	S	130	1	<0.1	23				1	<0.1	26
Sillago burrus	S	190	1	<0.1	23				1	<0.1	26
Atherinomorus ogilbyi	O	125	1	<0.1	23				1	<0.1	26
Acanthopagrus butcheri	E	110-354				26	1.4	6	26	0.8	13
Amniataba caudavittata	E	124-128				3	0.2	10	3	<0.1	21
Rhabdosargus sarba	O	144-223				3	0.2	10	3	<0.1	21
Carcharhinus leucas	S	1020				1	<0.1	12	1	<0.1	26
Total number of species				**26**			**13**			**30**	
Total number of fish				**1146**			**1923**			**3069**	

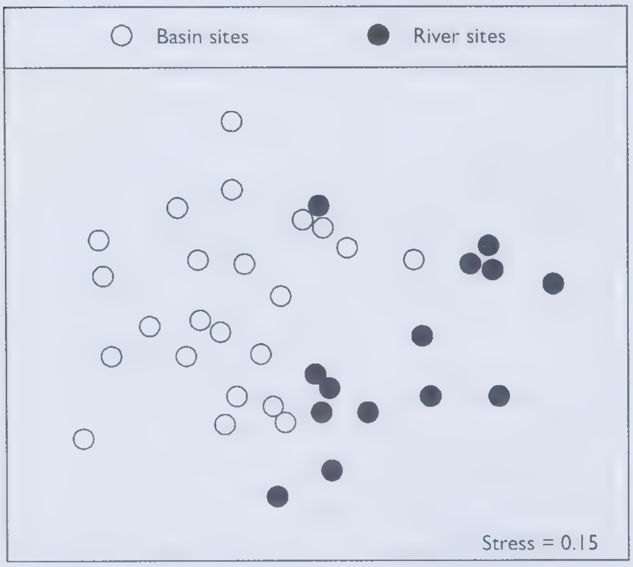

Figure 4. MDS ordination of the catch rates for each fish species in offshore, deeper waters of the basin and Collie River regions of the Leschenault Estuary between September 1993 and July 1994.

Leschenault Estuary. Furthermore, the initial appearance of small 0+ recruits in early autumn indicates that this species spawns in summer. Although the new 0+ age class of *F. lateralis* was not caught by Lenanton (1977) as early as March in the Blackwood River Estuary, the trends exhibited by length-frequency data for this species in that system otherwise closely parallel those described above for the Leschenault Estuary.

As with *Favonigobius lateralis*, the trends exhibited by length-frequency data for *Atherinosoma elongata* (not shown) indicate that this species, which reached a maximum length of only 87 mm (Table 2), also typically has a one year life cycle. This conclusion is based on the fact that the smallest fish, representing 0+ recruits, appeared in samples collected in summer and early autumn, and that the contribution made by larger fish subsequently declined markedly in the immediately ensuing months. These implications that *A. elongata* spawns in summer and has a one year life cycle are consistent with data recorded for this species in the Swan River Estuary (Prince & Potter 1983).

The trends exhibited by length-frequency data for

Leptatherina presbyteroides in the Swan River Estuary were the least well defined of the four smallest species of atherinid in that system (Prince & Potter 1983). The less clear trends for this species were regarded by Prince & Potter (1983) as attributable to the influence of spawning occurring at two different times of the year and/or to the incursion of representatives of marine populations of this species. Length-frequency data for this atherinid show that (1) this species rarely attains 60 mm in length in Leschenault Estuary, (2) its smallest representatives are found in summer and (3) its larger representatives decline in numbers in autumn and early winter. There thus seems every likelihood that, as in the Swan River Estuary, *L. presbyteroides* also typically has a one year life cycle in the Leschenault Estuary.

Table 6. Number (N), percentage contribution (%) and ranking by abundance (R) of each family of elasmobranch and teleost caught using gill nets in offshore, deeper waters of the Leschenault Estuary basin and Collie River and for both of these regions combined, based on data collected in September 1993 to July 1994 and May 1982 to February 1983.

Families	Basin			River			Basin and river		
	N	%	R	N	%	R	N	%	R
Mugilidae	346	30.2	1	432	22.5	2	778	25.4	2
Clupeidae	208	18.2	2	1325	68.9	1	1533	50.0	1
Pomatomidae	140	12.2	3	69	3.6	3	209	6.8	3
Arripidae	107	9.3	4				107	3.5	4
Sillaginidae	99	8.6	5	5	0.3	8	104	3.4	5
Carangidae	60	5.2	6				60	2.0	6
Terapontidae	50	4.4	7	3	0.2	9	53	1.7	7
Myliobatidae	32	2.8	8				32	1.0	10
Plotosidae	27	2.4	9				27	0.9	11
Tetraodontidae	18	1.6	10	1	<0.1	10	19	0.6	14
Engraulididae	14	1.2	11	8	0.4	7	22	0.7	13
Sciaenidae	13	1.1	12	32	1.7	4	45	1.5	8
Sparidae	9	0.8	13	29	1.5	5	38	1.2	9
Hemiramphidae	8	0.7	14				8	0.3	15
Gerreidae	5	0.4	15	18	0.9	6	23	0.7	12
Dasyatididae	3	0.3	16				3	<0.1	16
Rhinobatidae	2	0.2	17				2	<0.1	17
Platycephalidae	2	0.2	17				2	<0.1	17
Atherinidae	1	<0.1	19				1	<0.1	19
Bothidae	1	<0.1	19				1	<0.1	19
Triakidae	1	<0.1	19				1	<0.1	19
Carcharhinidae				1	<0.1	10	1	<0.1	19
Total number of families		21			11			22	
Total number of Fish		1146			1923			3069	

Table 7. Number (N) and percentage contribution (%) of species and individuals to each life cycle category caught using gill nets in offshore, deeper waters of the Leschenault Estuary basin and Collie River and for both of these regions combined, based on data collected in September 1993 to July 1994 and May 1982 to February 1983.

Life cycle category	Basin		River		Basin & River	
	N	%	N	%	N	%
Species						
Marine straggler	6	23.1	1	7.7	7	23.3
Marine estuarine-opportunist	17	65.4	8	61.5	18	60.0
Estuarine & marine	2	7.7	1	7.7	2	6.7
Estuarine	0	0	2	15.4	2	6.7
Semi-anadromous	1	3.8	1	7.7	1	3.3
Total	**26**		**13**		**30**	
Individuals						
Marine straggler	10	0.9	1	0.1	10	0.3
Marine estuarine-opportunist	887	77.4	560	29.1	1447	47.1
Estuarine & marine	41	3.6	8	0.4	49	1.6
Estuarine	0	0	29	1.5	29	0.9
Semi-anadromous	208	18.2	1325	68.9	1533	50.0
Total	**1146**		**1923**		**3069**	

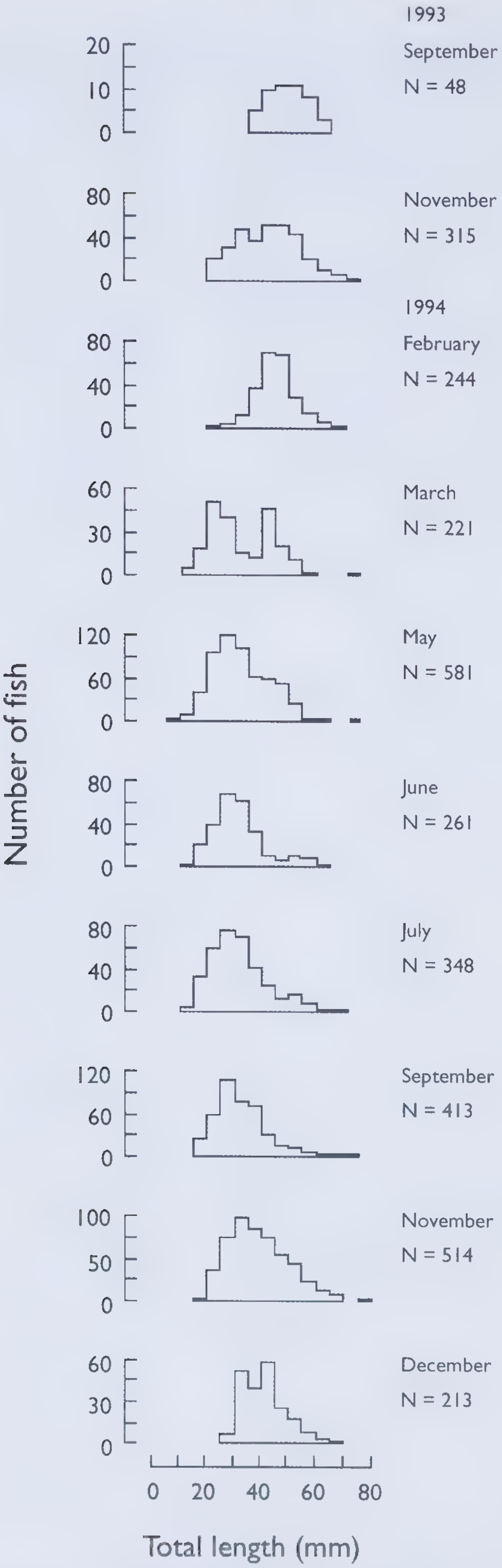

Figure 5. Length-frequency histograms for *Favonigobius lateralis*, derived using data obtained from samples collected by 21.5 and 41.5 m seine nets throughout the nearshore, shallow waters of the basin of Leschenault Estuary between September 1993 and December 1994. The numbers of fish used to construct the histograms for each month are given in italics.

The initial appearance of 0+ recruits of the yellow-eye mullet *Aldrichetta forsteri* in May, in which month their lengths lay between 20 and 49 mm (Fig 6), parallels the situation in the Swan River Estuary (Chubb *et al.* 1981). The presence of small *A. forsteri*, *i.e.* < 30 mm, in samples obtained between May and September is also consistent with the conclusion that, in south-western Australia, this species has a protracted spawning period that extends from early autumn to late winter or even early spring. This essentially parallels the situation elsewhere in south-western Australia (Thomson 1957b; Chubb *et al.* 1981). The modal length class of the 0+ cohort increased from 30-39 mm in May, to 40-49 mm in August, to 50-59 mm in November, and to 130-139 mm in March (Fig 6). There was thus a period of rapid growth between mid-spring and early summer. The pronounced bimodality of the 0+ age class in February, with modal length classes of 70-79 and 120-129 mm, which was a feature of some of the samples of this species collected in the Swan River and Peel Harvey estuaries (Chubb *et al.* 1981; Lenanton *et al.* 1984), was due to the presence of two groups of 0+ fish in February 1983. This implies that two pulses of different-sized new 0+ recruits, resulting from the 1982 spawning season, entered the Leschenault Estuary in 1982/83.

Three well-defined length distributions are present in the length-frequency data for *Aldrichetta forsteri* in May (Fig 6). The first comprised 0+ fish with a modal length of 30-39 mm (see above), compared with 140-149 and 220-229 mm for the second and third groups, respectively. On the basis of ageing studies carried out on *A. forsteri* in the Swan River Estuary (Chubb *et al.* 1981), these latter two groups are assumed to represent the early 1+ and early 2+ age classes, respectively. The modal length class of the presumed 1+ fish did not increase markedly between May and August, but then increased from 180-189 mm in August to 200-209 mm in February (Fig 6). The modal length class of the presumed 2+ fish in August was 220-229 mm and was thus similar to that in May. This age class was not well represented in subsequent months.

As with yellow-eye mullet, the new 0+ recruits of the sea mullet *Mugil cephalus* first appeared in May, in which month the lengths of virtually all of these fish lay between 20 and 39 mm (Fig 6). Small fish, *i.e.* < 30 mm, were also found until September, which essentially parallels the situation for *M. cephalus* in the Swan River and Peel Harvey estuaries (Chubb *et al.* 1981; Lenanton *et al.* 1984). The recruitment of small juvenile sea mullet over these several months is consistent with the conclusion that, in south-western Australia, this species spawns over a protracted period from early autumn to early spring (Thomson 1957b; Chubb *et al.* 1981). The modal length class of the 0+ fish increased from 30-39 mm in May and August to 60-69 mm in November to 70-79 mm in December and 170-179 mm in February (Fig 6). A massive growth of sea mullet over summer has also been recorded for this species in the Swan River Estuary (Chubb *et al.* 1981).

On the basis of ageing studies carried out on *Mugil cephalus* in the Swan River Estuary (Chubb *et al.* 1981), the second well-defined size group present in some months represented the 1+ age class (Fig 6). The modal length class of this cohort increased from 180-189 mm in May and August to 190-199 mm in November. The size of the 0+ fish in

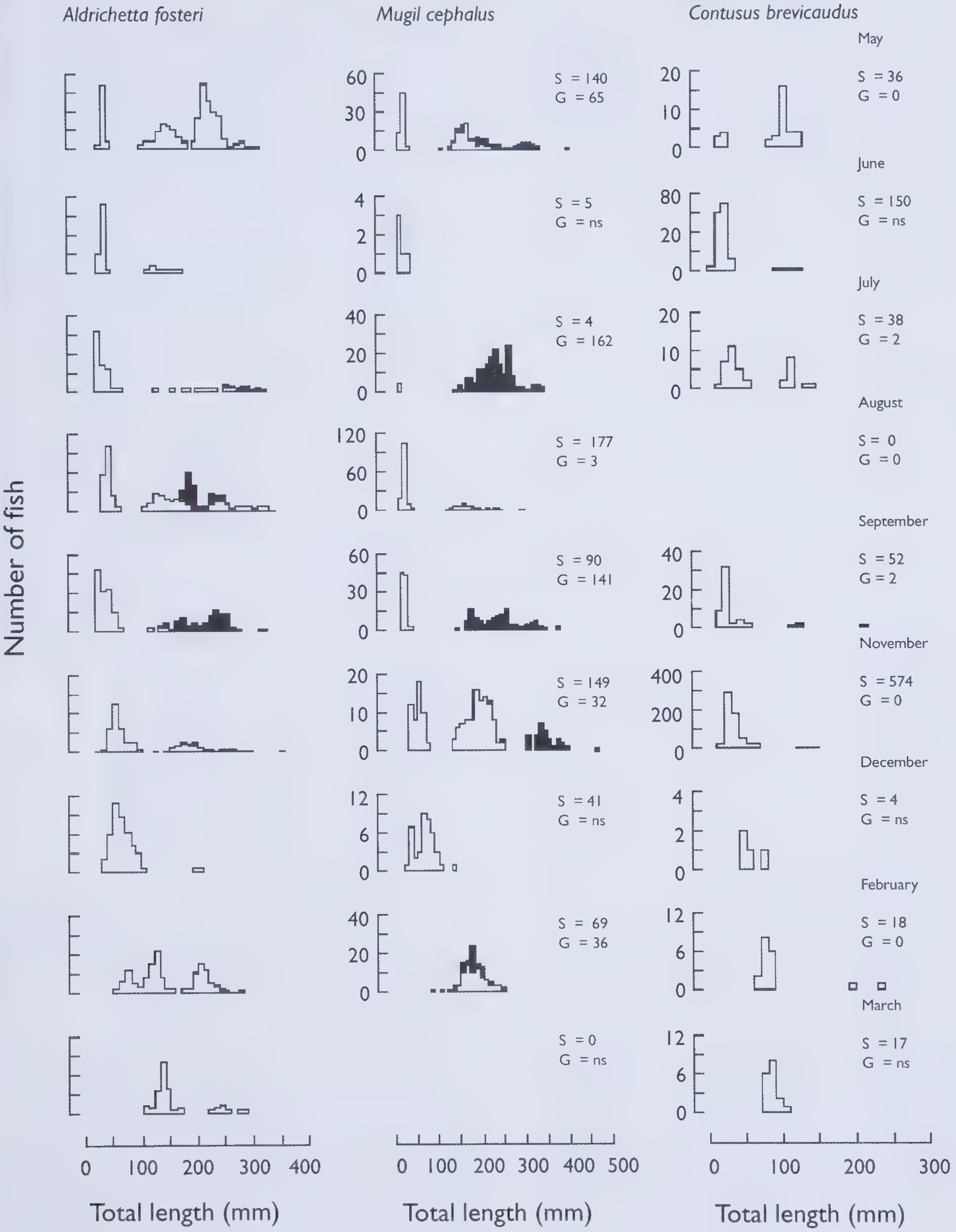

Figure 6. Length-frequency histograms for *Aldrichetta forsteri*, *Mugil cephalus* and *Contusus brevicaudus*. In this and Figs 7 and 8, data for the corresponding months of the year using both seine and gill nets in the basin and river regions of Leschenault Estuary in 1993/94 and 1982/83 have been pooled. In this and Figs 7-9, the numbers in italics for each month refer to the numbers of fish caught using seine (S; ☐) and gill (G; ■) nets. ns, not sampled. Data are provided only for these months in which an appreciable total number of fish were caught.

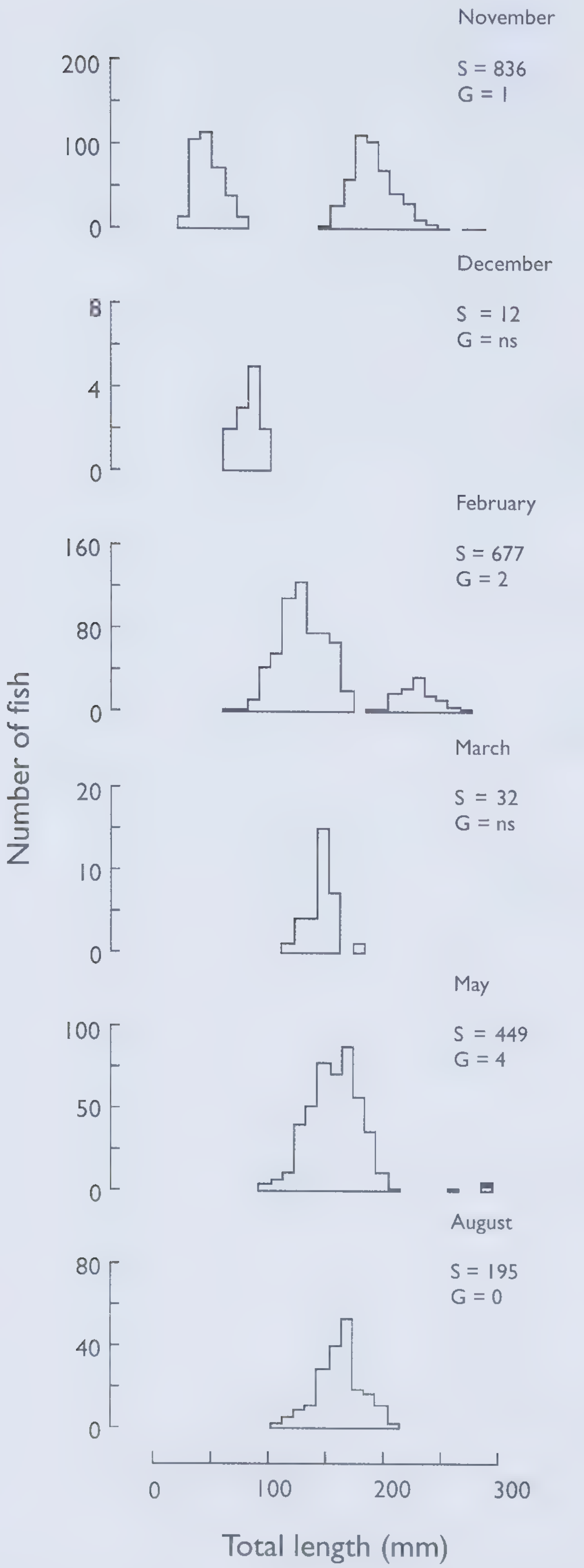

Figure 7. Length-frequency histograms for *Sillaginodes punctata*, caught by seine (S; ☐) or gill net (G; ■). ns, not sampled.

May is slightly less than that of the corresponding age class in both the Swan River and Peel Harvey estuaries in that month (Chubb *et al.* 1981; Lenanton *et al.* 1984). The third size group, with modal length classes between 310 and 340 mm in May, September and November, presumably represents the 2+ age class (Fig 6).

The new 0+ recruits of the prickly toadfish *Contusus brevicaudus* first appeared in May at lengths of only 20-39 mm (Fig 6), which implies that this species spawns in late summer and/or early autumn. The modal length class of the corresponding cohort remained between 30 and 49 mm from May to November, after which it increased to 80-89 mm in February and 110-119 mm in May and 120-129 mm in July. Assuming that spawning occurs in late summer, the fish in July would have been nearly 18 months old. The two largest fish by far were those with lengths of 199 and 239 mm, which were caught in February and were probably about two years old.

The first small 0+ recruits of the King George whiting *Sillaginodes punctata* appeared in the samples collected in November (Fig 7). These juveniles were small, ranging in length from 20 to 79 mm and producing a modal class at 40-49 mm (Fig 7). The latter size interval encompasses the modal length class recorded by Hyndes *et al.* (1998) for 0+ recruits of this species in the same month in coastal waters further north. The initial appearance of small 0+ recruits in Leschenault Estuary in November is consistent with the fact that, in south-western Australia, this species spawns between June and September (Hyndes *et al.* 1998). The modal length class of the 0+ age class increased from 40-49 mm in November to 120-129 mm in February and 140-149 mm in March (Fig 7). The modal length class of the corresponding cohort in August, now representing early 1+ fish, was 160-169 mm and was thus the same as that of the 0+ age class in May, demonstrating that *S. punctata* undergoes little growth during winter. The modal length class of 1+ fish increased from 160-169 mm in August to 170-179 mm in November and 220-229 mm in February (Fig 7). The largest King George whiting caught was 280 mm.

Two well-defined size groups were present in the length-frequency data for *Sillago schomburgkii* collected in February, May and August, the first having lengths ranging from 40-109 mm (Fig 8). Although the modal length class in February, *i.e.* 80-89 mm, was greater than in May and August, *i.e.* 60-69 mm, it should be recognised that the modal length class was skewed to the left in the latter two months. On the basis of ageing studies carried out on yellow-finned whiting in coastal waters further north (Hyndes & Potter 1997), this cohort clearly represents the 0+ recruits that result from the December to February spawning season of this species. The modal length classes of the group of larger *S. schomburgkii*, which are assumed to represent predominantly 1+ fish (see Hyndes & Potter 1997), increased from 150-159 mm in February to between 200 and 229 mm in May, August and November (Fig 8). The lengths of the presumed 1+ fish in other months are comparable to those recorded for this age class in coastal waters further north (Hyndes & Potter 1997).

Length-frequency data demonstrate that the lengths of the vast majority of the Perth herring *Nematalosa* *vlaminghi* that were caught in Leschenault Estuary in each month produced a modal class of *ca* 250 mm, except in February, when there also was a group of smaller fish with a modal length class of 160-169 mm (Fig 8). The situation in Leschenault Estuary thus contrasts markedly with that in the Swan River Estuary, where most of the fish are less than 200 mm in length and where a strong cohort of 0+ *N. vlaminghi* is frequently present (Chubb & Potter 1986). The data for the Swan River Estuary demonstrate that, during spring and summer, the sexually-maturing *N. vlaminghi* migrate into the saline reaches of the Swan River (upper Swan River Estuary) where spawning occurs. The 0+ fish then disperse downstream in the upper estuary and thence into the large basins that constitute the middle estuary (Chubb & Potter 1984). Since there are few areas of shallow banks in the lower reaches of the Collie River, and this river opens directly opposite to and not far from the very short entrance channel of the estuary, it is proposed that, unlike the situation in the Swan River Estuary, the 0+ *N. vlaminghi* soon move out of Leschenault Estuary and into marine waters. Moreover, this species apparently does not return to the Leschenault Estuary until it has reached the size at which sexual maturity is attained.

Any interpretation of the length-frequency data for the tailor *Pomatomus saltatrix* in south-western Australia must take into account the fact that the monthly trends exhibited by gonadosomatic indices (Lenanton *et al.* 1996) and the recruitment patterns of the 0+ age class (Lenanton *et al.*, Fisheries WA, unpublished data) provide strong circumstantial evidence that this species spawns twice annually in this region. The first spawning apparently peaks in early summer, while the second appears to peak in mid- to late autumn. It is thus proposed that the group of small fish with a modal length class of 50-59 mm in February (Fig 8) was the product of a summer spawning. The modal length class of the corresponding cohort was 60-69 mm in May and 80-89 mm in August and November. However, the mode of the 0+ cohort in November 1982 was skewed slightly to the left and was thus not fully representative in that month. The lack of recruitment of small fish, *i.e.* < 60 mm, in both August and November implies either that the autumn-spawning group had limited success in 1983 or that conditions were not conducive for recruitment of the 0+ age class into the Leschenault Estuary in that year. Since none of the fish in Leschenault Estuary were aged, it is not possible to determine whether or not the well-defined modes for larger fish were related to pulses of recruitment from either the product of an autumn or spring spawning cohort or of both cohorts.

The patterns just described for the length-frequency data for 0+ *Pomatomus saltatrix* in Leschenault Estuary contrast with those recorded for the Peel Harvey Estuary further north (Potter *et al.* 1983). Thus, while, as in the Leschenault Estuary, there were some small *P. saltatrix* in the Peel Harvey Estuary in February, there was, in that latter system in that month, also a second and larger group, with lengths ranging from 60-109 mm and having a modal length class of 90-99 mm, which was not represented in the Leschenault Estuary. Since this latter group clearly corresponded to the cohort that was recruited into the Peel Harvey Estuary in December, when the lengths ranged from 30-49 mm, it is believed to represent the product of an autumn rather than summer spawning. Thus, in February, the 0+ age class of *P. saltatrix* in the Peel Harvey Estuary was represented by a small group of fish that had apparently been spawned in summer and a larger group of larger fish that appeared to have been spawned in autumn. Furthermore, the growth of the 0+ cohort that appeared in the Peel Harvey Estuary in December, and which was apparently the result of an autumn spawning, was far more rapid than that described above for the 0+ age class that appeared in Leschenault Estuary in February, and which was apparently the product of an early summer spawning. Thus, in the case of that 0+ age class in the Peel Harvey Estuary, the modal length class increased rapidly from 50-59 mm in December to 90-99 mm in February and to 120-129 mm in March.

Virtually all of the sea garfish, *Hyporhamphus melanochir*, that were obtained during 1993/94 and 1982/83, were collected in May 1983. The 296 representatives of this species caught in that month constituted three well-defined size categories, with modal length classes of 110-119, 240-249 and 350-359 mm (Fig 9), which probably represent the 0+, 1+ and 2+ age classes, respectively.

Diets of fish

Chalmer & Scott (1984) showed that the Leschenault Estuary contained a range of benthic invertebrates, which were dominated by an abundance of bivalve molluscs, polychaetes and amphipods. They also showed that, on the basis of the diets of fish collected from both the Leschenault and nearby Peel Harvey estuaries, relatively large volumes of bivalve molluscs were consumed by species such as *Cnidoglanis macrocephalus, Gerres subfasciatus, Aldrichetta forsteri* and *Torquigener pleurogramma* and that polychaetes constituted an important component of the diets of *Sillaginodes punctata, Sillago schomburgkii, Arripis georgiana* and *A. forsteri*. Appreciable numbers of small crustaceans, such as amphipods and isopods, were ingested by *C. macrocephalus, A. caudavittata, A. forsteri* and *T. pleurogramma*, while larger crustaceans, such as the decapods *Palaemonetes australis* and *Alpheus* spp, were consumed by *A. caudavittata, S. schomburgkii, Pomatomus saltatrix* and *Argyrosomus japonicus* (formerly *Argyrosomus hololepidotus*). The last two species also fed on small fish, particularly *Engraulis australis*, and chironomid larvae constituted an important component of the diet of *A. forsteri*.

On the basis of their analyses of the gut contents of the above species, Chalmer & Scott (1984) considered that the feeding modes of the fish they examined in Leschenault Estuary comprised the following four main categories, namely (1) herbivores, (2) omnivores, (3) lower-order carnivores and (4) higher-order carnivores (Table 8). Since *Mugil cephalus* and *Nematalosa vlaminghi* feed predominantly on detritus (Thomson 1957c), a further category for detritivores is added to that list of four categories (Table 8).

The above fish species examined by Chalmer & Scott (1984) all grew to a relatively large size in Leschenault Estuary. On the basis of work carried out in the Swan River Estuary and Wilson Inlet, the far smaller species *Favonigobius lateralis* would be expected to feed mainly on polychaetes and amphipod crustaceans, together with some detritus (Gill & Potter 1993; Humphries & Potter 1993).

Studies in those other two estuaries also suggest that, in Leschenault Estuary, the atherinid *Atherinosoma elongata* would probably feed largely on benthic prey, such as polychaetes and certain crustaceans, *e.g. Palaemonetes australis*, and on detritus, whereas the other small atherinid *Leptatherina presbyteroides* would probably feed on planktonic crustaceans, such as calanoid and harpacticoid copepods, terrestrial insects, larval bivalves and foraminiferans (Prince *et al.* 1982; Humphries & Potter 1993).

Commercial fishery

The number of commercial fishing boats that were operating annually in Leschenault Estuary between 1981 and 1997 declined from a maximum of 21 in 1982 to 6 or 7 boats in 1993 to 1997 (Fig 10 a). This decline in the number of boats fishing between the early 1980s and mid 1990s is a direct consequence of the long term policy of Fisheries Western Australia to allow the level of participation by commercial fishers in the Leschenault Estuary to undergo

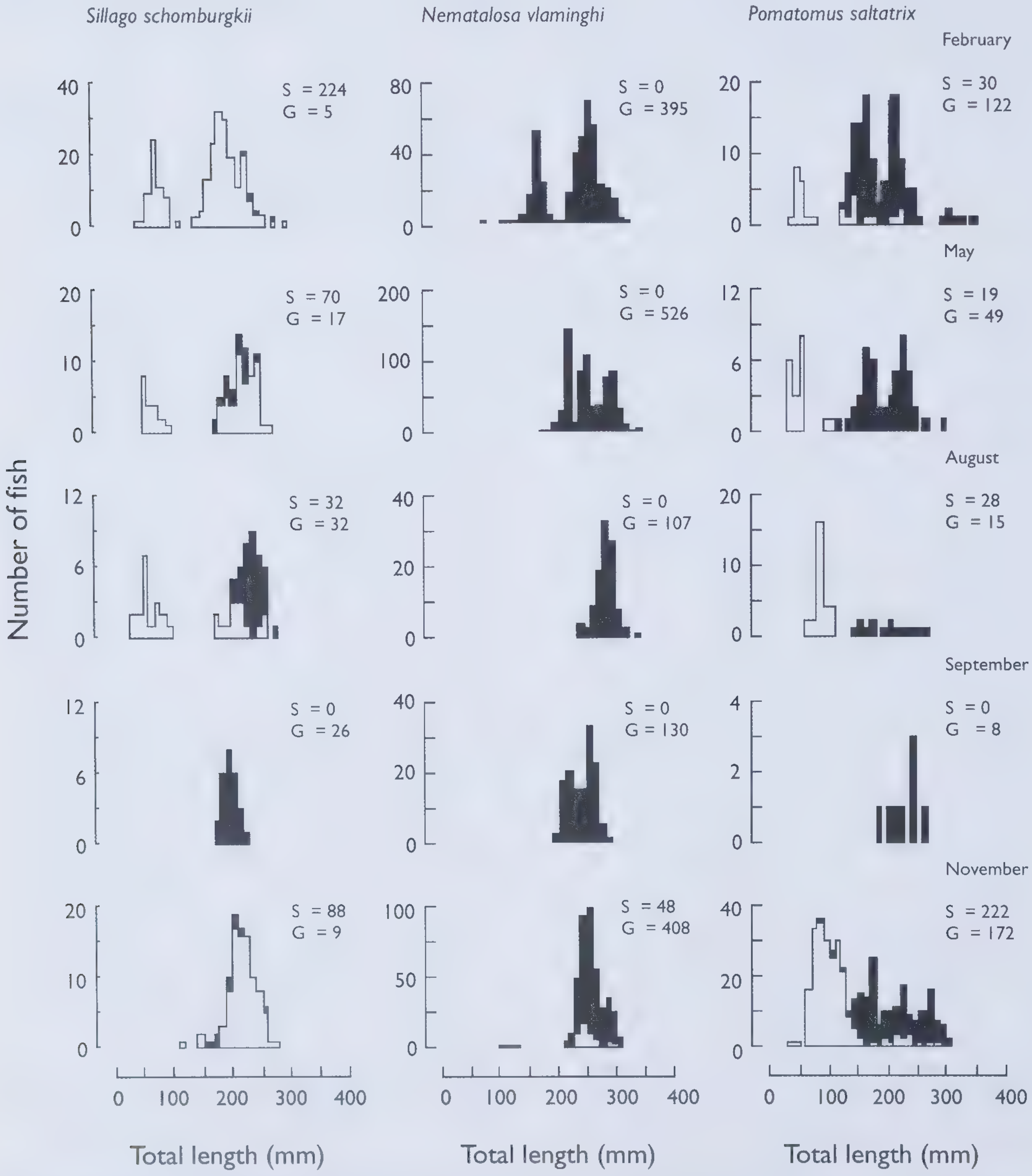

Figure 8. Length-frequency histograms for *Sillago schomburgkii, Nematalosa vlaminghi* and *Pomatomus saltatrix,* caught by seine (S; ☐) and gill net (G; ■).

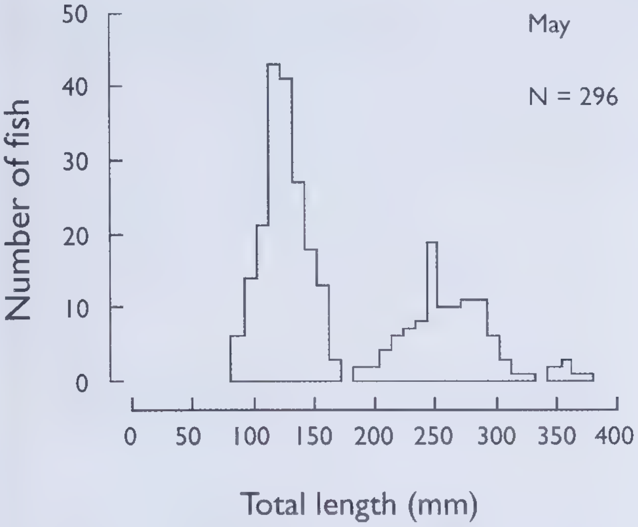

Figure 9. Length-frequency histograms for *Hyporhamphus melanochir* derived from samples collected by seine and gill nets in the basin of the Leschenault Estuary in May 1982.

a progressive reduction. In other words, the license of a commercial fisher is allowed to lapse when that fisher decided to leave the industry.

The amount of gill net effort reported in the years between the early 1980s and 1997 declined markedly and progressively from its maximum of 831 boat days in 1981 to less than 90 boat days in 1991 to 1997 (Fig 10 B). The amount of annual haul net effort between 1981 and 1987 was essentially the same as that of gill net effort, *i.e.* with annual values ranging from 375 to 780 boat days. However, unlike the situation with gill net effort, the haul net effort did not decrease after 1987, remaining above 500 boat days in these subsequent years. The fact that haul net effort greatly exceeded that of gill net effort during the 1990s reflects a deliberate policy, that was instigated by the commercial fishers, to use a technique that would both reduce the amount of bycatch and overcome the problems posed to other users of the estuary by nets being left unattended overnight in the water.

When gill and haul net effort were combined, the resultant total effort reported by commercial fishers can be seen to have declined from greater than 1 300 boat days between 1981 and 1984, to about 850 boat days in all but one year between 1985 and 1990 and then to less than 700 boat days in subsequent years (Fig 10 C). The substantial decline in both the number of boats operating and total fishing effort is reflected in the total reported catch of finfish species. Thus, the wet weight of catch was typically greater than 150 000 kg in 1981 to 1985, compared with *ca* 10 000 kg in 1986 to 1992 and *ca* 85 000 kg in 1993 to 1997 (Fig 10 D).

The catches of the main commercial fish species in Leschenault Estuary were derived from statutory monthly returns sent to Fisheries Western Australia. Discussions with commercial fishers suggest that, prior to 1989, some of the catches obtained in Koombana Bay for some species in a minority of months may have been inadvertently coded as having been taken in Leschenault Estuary and that the catches of yellow-eye mullet *Aldrichetta forsteri* and sea mullet *Mugil cephalus* within the estuary may, in some cases, have been confused. However, it is clear from discussions with commercial fishers that the ranking, in terms of weight of catch that is given for the different species in Table 9 and the overall trends shown for the annual catches of those species in Fig 11, are broadly valid.

Six species of finfish, *i.e. Aldrichetta forsteri, Mugil cephalus, Sillago schomburgkii, Sillaginodes punctata, Cnidoglanis macrocephalus* and *Hyporhamphus melanochir,* were caught in Leschenault Estuary by commercial fishers in each of the 17 years between 1981 and 1997 (Table 9). *Nematalosa vlaminghi* and *Pomatomus saltatrix* were caught in most of those years and *Acanthopagrus butcheri* was caught in nine of those years.

In terms of wet weight, *Aldrichetta forsteri* was the most important commercial finfish species in Leschenault Estu-

Table 8. Modes of feeding of the main fish species in Leschenault Estuary and their major dietary components.

Mode of feeding	Species	Major dietary components
Herbivores	*Hyporhamphus melanochir, Pelates sexlineatus*	Green and brown algae
Detritivores	*Mugil cephalus, Nematalosa vlaminghi*	Bottom sediment, detritus
Omnivores	*Aldrichetta forsteri, Amniataba caudavittata*	Algae, bivalve molluscs, isopods, decapods, *e.g. Palaemonetes australis,* insect larvae, *e.g.* chironomids, polychaetes
Lower-order carnivores	*Favonigobius lateralis, Leptatherina presbyteroides Atherinosoma elongata, Sillaginodes punctata, Gerres subfasciatus, Torquigener pleurogramma, Sillago schomburgkii, Cnidoglanis macrocephalus,*	Small crustaceans, *e.g.* amphipods, and large crustaceans, *e.g. Palaemonetes australis* and *Alpheus* spp, bivalve molluscs, polychaetes
Higher-order carnivores	*Argyrosomus japonicus, Pomatomus saltatrix*	Juveniles of other fish species, smaller fish species, *e.g. Engraulis australis,* and larger crustaceans, *e.g. Palaemonetes australis*

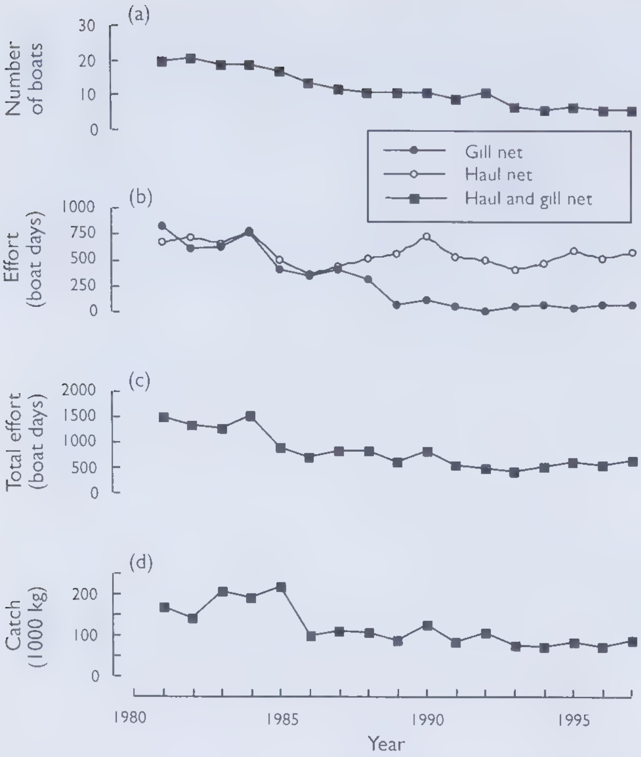

Figure 10. Data on the commercial fishery in the basin of the Leschenault Estuary in each year between 1981 and 1997. (A) number of boats fishing, (B) number of days spent fishing using gill and haul nets, (C) total effort and (D) total catch of finfish.

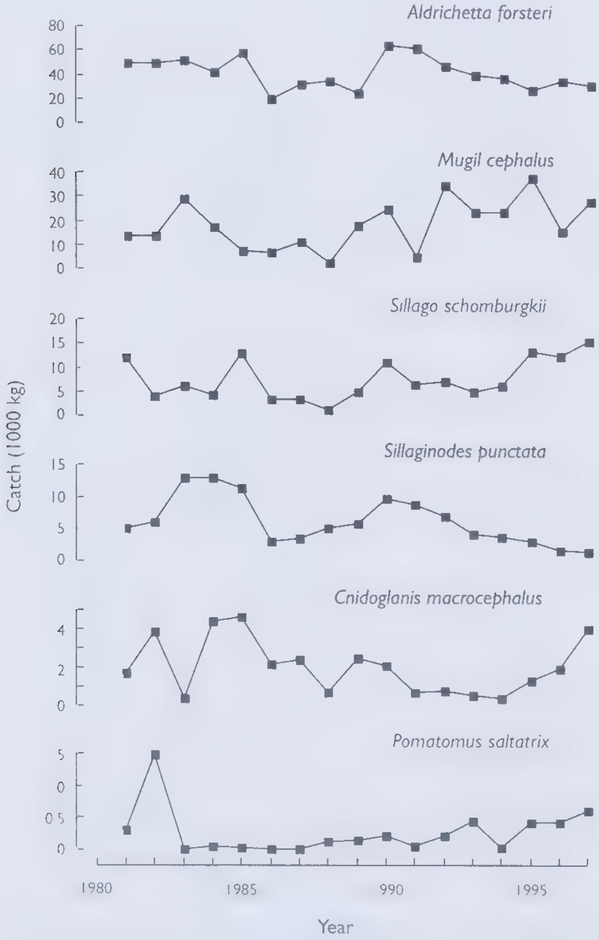

Figure 11. Total annual catches of the main finfish species in the Leschenault Estuary between 1981 and 1997.

ary, with a mean annual catch of 65 255 kg and a contribution of *ca* 56% to the total wet weight of all finfish caught in the 17 years between 1981 and 1997 (Table 9). The next most important species during those years were *Mugil cephalus, Sillago schomburgkii, Sillaginodes punctata* and *Nematalosa vlaminghi*, with mean annual contributions of between 3.6 and 20.2% to that total wet weight. *Cnidoglanis macrocephalus* contributed only 2.0% to the total wet weight over the above period and *Pomatomus saltatrix, Hyporhamphus melanochir* and *Acanthopagrus butcheri* each contributed less than 0.5% (Table 9).

The maximum annual catches of the three species that contribute most to the total catch were *ca* 65 000 kg for *Aldrichetta forsteri* in 1990, *ca* 37 000 kg for *Mugil cephalus* in 1995 and *ca* 16 000 kg for *Sillago schomburgkii* in 1997 (Fig 11). The annual catches of each of the other three main fish species varied markedly between 1981 and 1997. The annual catches of *Sillaginodes punctata* and *Cnidoglanis macrocephalus* reached maxima of *ca* 13 500 and 4 500 kg, respectively.

The decline undergone by catches of *Aldrichetta forsteri* during recent years contrasts with the maintenance of the catches of *Mugil cephalus* during that same period (Fig 11). This difference in trends reflects the fact that, while there has been a decline in the demand for mullets in general as bait for the rock lobster industry, there has still been a demand for sea mullet (but not yellow-eye mullet) as a food fish. During recent years, the catches of *Sillaginodes punctata* have declined while those of *Sillago schomburgkii* have risen, reflecting a targetting of the latter species due to a shortage of the former species. This decline in the catches of *S. punctata*, which contrasts with the situation elsewhere in south-western Australia, may be related to the deleterious effects that would almost certainly have been caused to fish nursery areas both by dredging in the harbour and through the deposition of dredge spoil along the coast northwards to the estuary mouth. The consistently relatively low catches of *C. macrocephalus* in most years since 1986 probably reflect the effects of strong fishing pressure on this species, coupled with the deleterious effects of a legal minimum length below the age at first maturity (Laurenson *et al.* 1993a,b), a situation which parallels that found in some other estuaries in south-western Australia (Steckis *et al.* 1995).

Recreational fishery

The preliminary data derived from a creel census carried out by Fisheries Western Australia demonstrated that the catches of recreational fishers in Leschenault Estuary during 1998 were dominated by the three species of whiting (*Sillaginodes punctata, Sillago schomburgkii* and *Sillago burrus*) and tailor (*Pomatomus saltatrix*). The next most abundant species were Australian herring (*Arripis georgiana*) and tarwhine (*Rhabdosargus sarba*). Smaller catches of several other species, including juvenile Australian salmon (*Arripis truttaceus*) and skipjack or southern trevally (*Pseudocaranx dentex*) and sizeable, incidental catches of toadfishes or pufferfishes (*Contusus brevicaudus* and *Torquigener pleurogramma*) were also obtained.

Table 9. List of main finfish species caught commercially in Leschenault Estuary, together with the numbers of years they were caught between 1981 and 1997, the total catch and mean annual catch (± 1se) for those years and the percentage contribution of each species to the total catch over that period.

Species	Years	Total catch, all years *(kg)*	Mean annual catch *(kg per year)*	Contribution (%)
Aldrichetta forsteri	17	1 109 343	65 255 (± 7875)	55.5
Mugil cephalus	17	404 248	23 779 (± 2547)	20.2
Sillago schomburgkii	17	220 762	12 986 (± 1833)	11.1
Sillaginodes punctata	17	132 332	7 784 (± 1208)	6.6
Nematalosa vlaminghi	13	71 448	5 496 (± 2040)	3.6
Cnidoglanis macrocephalus	17	39 485	2 323 (± 383)	2.0
Pomatomus saltatrix	16	7 759	485 (± 239)	0.4
Hyporhamphus melanochir	17	6 859	403 (± 75)	0.3
Acanthopagrus butcheri	9	5 106	567 (± 217)	0.3

Conclusions

The collation of unpublished and published data in this paper shows that Leschenault Estuary is used as a nursery area by several marine fish species, including *Hyperlophus vittatus, Aldrichetta forsteri, Mugil cephalus, Sillago schomburgkii, Sillaginodes punctata, Sillago burrus, Pomatomus saltatrix, Gymnapistes marmoratus, Contusus brevicaudus* and *Torquigener pleurogramma*. The nursery function provided by this estuary parallels that afforded to certain marine species by comparable areas in estuaries elsewhere in south-western Australia (Potter & Hyndes 1999) and in temperate regions of the northern hemisphere (Haedrich 1983; Dando 1984; Kennish 1990). However, unlike the situation frequently found in temperate holarctic estuaries, such as that of the Severn River in England (Claridge *et al*. 1986), the 0+ age class of these species in south-western Australian estuaries remains strongly represented throughout the year in Leschenault Estuary. Furthermore, the above species are also usually well represented throughout the year by the 1+ and also sometimes the 2+ and even older age classes. This parallels the situation in estuaries such as the Peel Harvey and Swan River estuaries to the north (Chubb *et al*. 1981; Lenanton *et al*. 1983; Potter *et al*. 1983) and in the Blackwood River Estuary to the south (Lenanton 1977). Estuaries provide excellent fish nursery areas because their high productivity (Schelske & Odum 1961) facilitates particularly rapid growth rates, which thereby soon makes juvenile fish less susceptible to predation (Kennish 1990). The high productivity of estuaries would also be of value to those species that spend the whole of their life cycles in estuaries. Furthermore, estuaries contain relatively far fewer large piscivorous predators than the natal environments of marine fish species (Blaber & Blaber 1980). The extensive growths of seagrasses in Leschenault Estuary, and particularly of *Halophila*, would also provide protection for small species from any potential predators. The high abundance of certain estuarine-spawning species in the shallows of Leschenault Estuary, together with the restriction of *Lesueurina platycephala* to the shallows of Koombana Bay, where it was relatively very abundant, help account for the marked differences in the compositions of the fish fauna in the shallows of the estuary and the bay.

The work of Chalmer & Scott (1984) demonstrated that Leschenault Estuary contains an abundance of the type of benthic fauna that forms a major component of the diets of fish species in this estuary, *e.g.* nereidid polychaetes, the bivalve *Arthritica semen* and amphipods of the genus *Paracorophium*. There are also extensive beds of seagrass (mainly *Halophila* species) which, together with the profuse algal covering, provide an abundance of food for herbivorous invertebrates and fish and result in the production of large amounts of detritus which constitutes an important component of the diets of certain benthic invertebrates and some teleost fish. Since the densities of potential invertebrate prey are far greater in Leschenault Estuary than Koombana Bay (P Chalmer, unpublished data), it seems highly relevant that the overall density of fish in shallow waters is far greater in the estuary than the bay.

Although the shallow waters of estuaries provide important nursery areas for certain marine fish species, the contribution of such fish to the total number of fish in these waters was less than half that of those species which complete their life cycle in the estuary, *i.e.* 32.1 *vs* 67.9%. The presence in Leschenault Estuary of very large numbers of individuals of estuarine species, such as the gobies *Favonigobius lateralis, Pseudogobius olorum* and *Afurcagobius suppositus*, the atherinids *Leptatherina presbyteroides, Atherinosoma elongata* and *Leptatherina wallacei*, and the gobbleguts *Apogon rueppellii*, is probably attributable to the presence of high and stable salinities during summer, when spawning occurs, and to the influence of landlocking and/or the limited exchange with the sea during the recent geological past (see introduction).

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Use of the Leschenault Inlet estuary by waterbirds

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Abstract

Leschenault Inlet estuary is a large, permanent estuary supporting a heterogenous array of habitats, giving the inlet the potential to support significant waterbird populations. Nine waterbird surveys were conducted in the estuary, including its fringing wetland area, and in some closely associated out-lying wetlands. During this 14 month study 23 565 waterbird records comprising 57 species were recorded between 1987 and 1988. The functional uses of the habitats within the estuary and out-lying wetlands were determined by analysing the numbers, species richness and behavioural activity of waterbirds in each habitat type. Analyses of these data, in combination with Birds Australia data-bases, indicate that Leschenault Inlet estuary is an important waterbird location within southern Western Australia and is likely to be a critical integral component of the wetland network used by waterbirds in this region. For example it is a dry season refuge for waterbirds in mid spring and summer and ranks amongst the top wetlands in the south west of the State in terms of species richness, numbers of waterbirds and numbers and richness of waterbird species scheduled under international migratory bird agreements. Locally, the out-lying wetlands appear to be a complementary part of a wider Leschenault wetland system. They support a wide variety of species, including five species not recorded in the estuary, with 71% of all breeding activity recorded. Waterbirds make extensive use of most habitats within the estuary and out-lying wetlands, often using them for different purposes. For example, in the estuary the open water habitats (*e.g.* sandbars and shallow water) support the larger part of the waterbird population and are largely used for feeding. However, the fringing wetland habitats (*e.g.* wet and dry salt marshes and pools) support a greater density and a larger variety of waterbirds. These wetlands are used equally for feeding and roosting and support significant breeding.

Keywords: Avifauna, avifauna habitats, Leschenault Inlet, estuary, south-western Australia.

Introduction

Leschenault Inlet estuary is located 135 km south of Perth, immediately north of Bunbury, Western Australia (Fig 1). The estuary is an elongate lagoonal estuarine system, separated from the Indian Ocean by the dunes of the Leschenault Peninsula. A narrow cut has been excavated at the southern end to allow greater exchange of ocean water. Within the estuary there are several large scale, tidal and subtidal geomorphic/bathymetric units, a poikilosaline range of salinity fields and a heterogeneous array of vegetation types across the system, including various forms of fringing vegetation (Wurm & Semeniuk 2000; Pen *et al.* 2000).

Given the variety of habitat types present, Leschenault Inlet estuary is likely to support a significant number of waterbird species. While the estuary has been included in a number of broad scale, comparative waterbird studies (Jaensch *et al.* 1988; Halse *et al.* 1990, 1992, 1995; Storey *et al.* 1993), the present paper describes the most detailed study of the waterbird usage of Leschenault Inlet estuary conducted to date.

In this study total counts were conducted over the whole estuary including the wetland fringes, which comprised wet and dry salt marsh, pools and bare shoreline. Some closely associated wetlands immediately east and south of the estuary were also included, but analysed separately. Nine surveys were conducted between September 1987 and October 1988, providing two samples per season except spring, which had three. Waterbird species, number, location, habitat type and behaviour were recorded for each observation. This study was originally designed to determine the importance of mosquito breeding areas to waterbirds (Ninox Wildlife consulting 1989). In this study the data have been re-analysed in an attempt to determine the likely ornithological value and functional use of Leschenault Inlet estuary and the small-scale habitats within it.

Methods

Study area

Leschenault Inlet estuary is one of the few large estuaries in southern Western Australia opening to the Indian Ocean (Fig 1). It is located on the south west coast of Western Australia and is the third largest estuary (2600 ha) between Hill River to the north and the Vase-Wonnerup Estuary to the south (Hesp 1984). The estuary is a permanent, microtidal (mean diurnal tide = 0.5 m), wave-dominated estuarine lagoon, with sea and land breezes and winter storms developing wind waves. Atmospheric pressure has a greater effect on water levels than astronomical tides, with summer high pressure systems resulting in low water and winter low pressure systems producing a small general rise in mean sea level (Semeniuk & Meagher 1981). The estuary is annually poikilosaline with a south to north salinity gradient, which is generally unstratified (Wurm & Semeniuk 2000).

Leschenault Inlet estuary has a deeper central basin

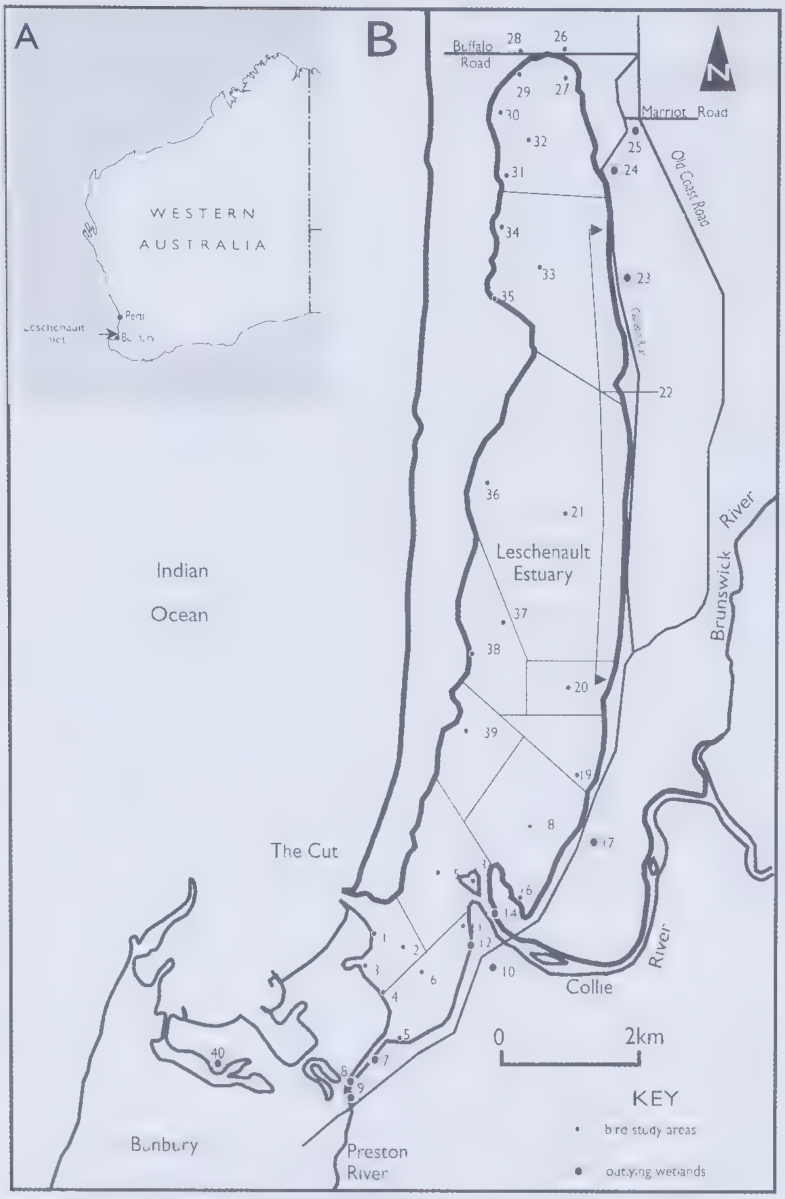

Figure 1. A. Locality of Leschenault Inlet estuary and outlying wetlands. B. Waterbird sampling areas.

(approximately 1 m) with shallower peripheral platforms and ramps. The estuary is composed of subtidal, tidal, and supratidal areas and can be divided into eight bathymetric and geomorphic units (Wurm & Semeniuk 2000). The estuary comprises open water habitats (deep water, shallow water, tidally exposed sandbars and mud flats) and fringing habitats (shoreline, salt marsh, pools, mangroves and paperbark thickets). For the purposes of the present study, these habitats and habitat elements such as perches (posts protruding from the water, rocks, tree branches), man-made drains, car parks, and grassed areas were divided into 13 habitat sub-units plus one miscellaneous category (Table 1). The sub-unit 'other fringing wetland habitat' was used to encompass diverse habitat elements such as fly-ash dumps, car parks, grassed areas, roads, and telephone poles found in the fringing wetlands.

Sampling

Thirty sites were selected to cover the whole Leschenault Inlet estuary area (Fig 1). In addition ten closely associated out-lying wetland areas were included because they were likely to be used by waterbirds using the estuary. Most of these sites were located on the east side of the estuary (sites 10, 12, 17, 23-25), one was on the south side (site 40) and three on the Preston River (sites 7-9). All sites comprised more than one habitat sub-unit. Site 40 was the only location having significant mangrove habitat and the only site for which the mangrove habitat sub-unit was used. Other minor mangrove habitat was included in the other habitat sub-units.

No attempt was made to scale the relative areas of habitat sub-units in individual wetlands since this varied from survey to sur-

Table 1. List of habitat sub-units used in this study.

Habitat Sub-Units	Description
Fringing Wetland Habitats	
Dry salt marsh	Supratidal samphire vegetated flat
Wet salt marsh	High tidal samphire vegetated flat
Pools (fringing wetland habitat)	Pools within high tidal vegetated flat
Bare shoreline	Mid-tidal flats bare of vegetation
Mangroves	Mangroves on mid to high tidal flats fronting steep dune shores
Drains	Man made drains within the fringing wetland habitat
Perches (fringing wetland habitat)	Perches in paperbark thickets, mangroves, dead trees and fence posts.
'Other' (fringing wetland habitat)	Grassed areas, roads, car parks, telephone poles, fly ash dumps
Open Water Habitats	
Deep water basin	Central basin of estuary and deeper parts of the platforms & ramps
Shallow water	Shallow sub-tidal and low tidal parts of the platforms and ramps
Tidal flats	High tidal flats without vegetation.
Sandbars	Beach ridges, spits, bar and lagoon shores
Perches (open water habitat)	Rocks protruding from the water, fence posts, and other man made objects within the open water habitat
Other (open water habitat)	Miscellaneous

vey depending on tide height. For example, an area of dry salt marsh observed during one survey could be inundated at the next survey, appearing as wet salt marsh or even a large pool. Scaling has therefore been limited to an overview of the estuary. The fringing wetland habitat in the estuary represents approximately 11% of the total estuary area, while the open water habitat represents approximately 89%. This will obviously vary with tides and fresh water inflows.

In this study waterbirds are defined as those bird species that are dependent on wetlands for their survival (Jaensch *et al.* 1988) and comprise various groups including waterfowl, shorebirds, crakes, rails and certain species of raptors and passerines (warblers). Four species of bird (domestic duck sp, Magpie-lark *Grallina cyanoleuca*, White-fronted Chat *Epthianura albifrons* and Richard's Pipit *Anthus novaeseelandiae*), recorded in the Ninox Wildlife Consulting (1989) surveys, were not included in this study because the domestic duck is not a native species and the other three birds are not reliant on these habitats. The nomenclature used in this study is according to Christidis & Boles (1994).

Sampling was conducted simultaneously by three field-staff working co-operatively with one another such that the combined samples could be viewed as a total census of the estuary and out-lying wetlands conducted within one day during day light hours. The dates of the nine surveys are given in Table 2. At a sampling site, the observer selected a vantage point, remaining there until confident that all visible birds had been identified, counted, allocated to habitats and their activity defined. Foot or vehicle transects were conducted between each sample site and spot-checks made along the way to ensure that all birds were recorded. Members of the more cryptic, secretive species, such as crakes and rails, may have been missed because different methods of survey are required to adequately sample these species. Behavioural activities recorded included feeding, roosting (any sort of land-based resting/sleeping), loafing (bird resting on water including directionless drifting), flying overhead, breeding (nesting or small young feeding) and 'other' (miscellaneous including preening and fighting). The functional use of each habitat sub-unit was determined by considering the numbers, species richness and behavioural activity of the waterbirds utilising them. The data from out-lying wetlands were analysed separately from the data from the estuary.

Table 2. Surveys conducted at Leschenault Inlet estuary and out-lying wetlands in 1987 and 1988.

SURVEY	DATE	SEASON
1	3 September 1987	Spring
2	29 October 1987	Spring
3	15 December 1987	Summer
4	4 February 1988	Summer
5	23 March 1988	Autumn
6	11 May 1988	Autumn
7	29 June 1988	Winter
8	4 August 1988	Winter
9	20 October 1988	Spring

To give the conservation values of Leschenault Inlet estuary and the out-lying wetlands a State perspective, the Birds Australia data bank on wetlands (Anon 1999) was consulted, and data collected from 1988 to 1999 was analysed. Over 700 wetlands in southern Western Australia were compared and ranked under the following parameters: total numbers of waterbirds recorded in any one survey, species richness, numbers and richness of species scheduled under international migratory bird agreements and richness of species that breed in the study site. The out-lying wetlands were assessed separately. As most of the out-lying wetlands were not included in the Birds Australia data bank (Anon 1999), unpublished data were used instead to make the State comparisons. Birds Australia and Ninox Wildlife Consulting (1989) data were considered together to determine the State perspective and seasonal use of the estuary and out-lying wetlands.

Results

Species richness and numbers of waterbirds

During the Ninox Wildlife Consulting (1989) study, 21 040 records of waterbirds comprising 50 species were

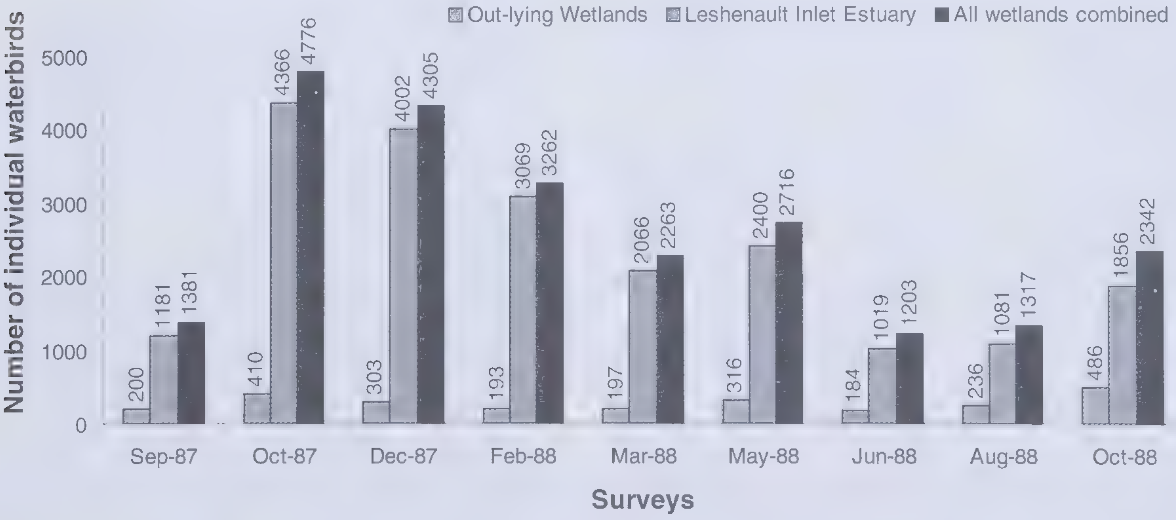

Figure 2. Number of individual waterbirds counted during surveys of the Leschenault Inlet estuary and outlying wetlands.

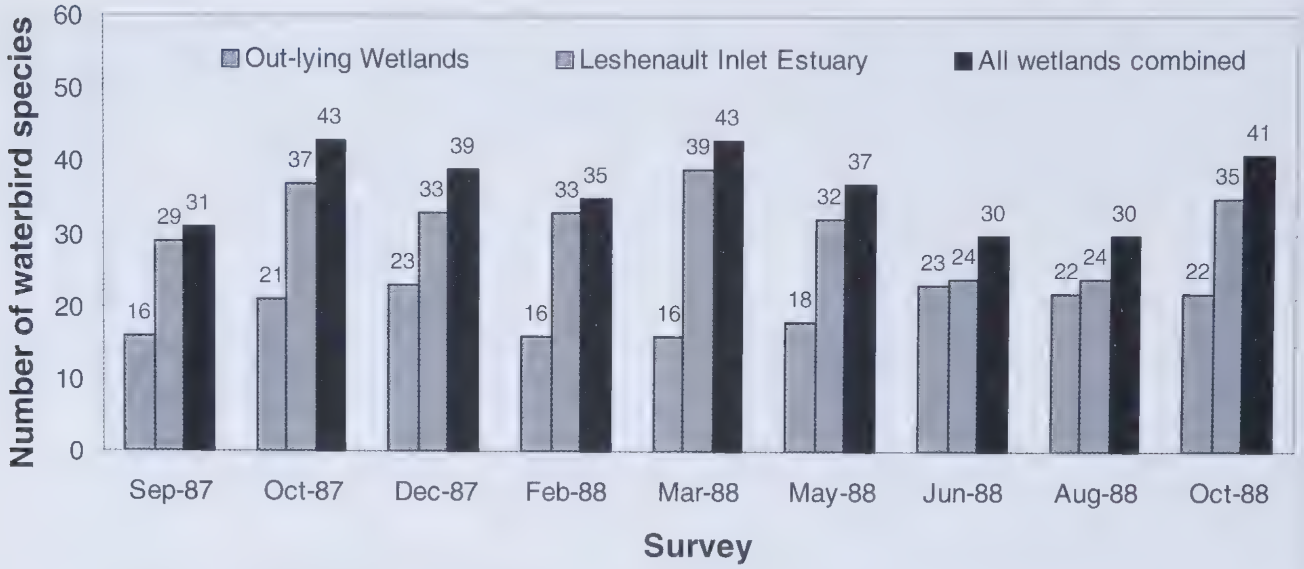

Figure 3. Species richness during surveys of the Leschenault Inlet estuary and outlying wetlands.

collected on the Leschenault Inlet estuary. During the nine samples taken over this 14 month study, the estuary was populated by 1 019-4 366 waterbirds comprising 24-39 species. Greatest numbers of waterbirds occurred on the estuary in mid-spring (when numbers for October 1987 and 1988 are averaged) and early summer, generally decreasing towards winter (Fig 2). Species richness was generally high throughout the year, but lowest during winter (Fig 3). An additional 2 525 waterbird records (10.7% from a total of 23 565 for the estuary and outlying wetlands) and seven species (12.2% from a total of 57) were contributed by sampling the closely associated outlying wetlands (sites 7-10, 12, 17, 23-25, 40). These areas were populated by 200-486 waterbirds comprising 16-23 species. Greatest numbers of waterbirds on these wetlands occurred in mid spring (mean for October 1987 and 1988), generally decreasing in numbers in mid summer through to winter (Fig 2). Few or no waterbirds occurred on many out-lying wetlands during summer and autumn. However, sites 7, 9 and 40 supported waterbirds throughout the year. Site 17 had waterbirds as late as February. Species richness was generally moderate throughout the year, but highest in mid to late spring and winter and lowest in late summer and autumn (Fig 3). A list of the species recorded in the estuary and out-lying wetlands is given in the Appendix.

Habitat use

In the Leschenault Inlet estuary the open water habitats (described in Table 1) together had 14 021 waterbird records (67% of the total waterbirds recorded in the estuary) comprising 43 species (86% of all species recorded in the estuary). The sub-units in the open water habitat were largely used for feeding (36.5% of behavioral activity re-

Table 3. Habitat sub-units of the Leschenault Inlet estuary ranked by abundance of waterbirds. Major behavioural activities in each sub-unit are also presented in order of prominence.

Habitat Sub-units in Estuary	Number of birds & % Abundance	Major Activity
*Deep water basin	3730 (17.7%)	Feed, Loaf
*Tidal flats	3161 (15.0%)	Roost, Feed
*Shallow water	2700 (12.8%)	Feed, Loaf
*Sandbars	2580 (12.2%)	Roost, Feed
Bare shoreline	2116 (10.0%)	Roost, Feed
Wet salt marsh	1905 (9.1%)	Feed, Roost
*Perches (open water habitat)	1449 (6.9%)	Roost
Pools (fringing habitat)	1413 (6.7%)	Feed, Loaf
Perches (fringing habitat)	743 (3.5%)	Roost
Dry salt marsh	499 (2.4%)	Roost
Other (fringing habitat)	337 (1.6%)	Roost, Fly
*Other (open water habitat)	401 (1.9%)	Other
Drains	6 (0.03%)	Feed, Other
Mangroves	n/a	n/a

* = open water habitat sub-units. n/a = not applicable to the estuary.

Table 4. Habitat sub-units of Leschenault Inlet estuary ranked by richness of waterbird species.

Habitat Sub-units in Estuary	Species Richness & % Total Species
Wet salt marsh	39 (78%)
Pools	33 (66%)
Bare shoreline	32 (64%)
*Deep water basin	29 (58%)
*Shallow water	29 (58%)
*Sandbars	27 (54%)
*Tidal flats	26 (52%)
Dry salt marsh	22 (44%)
Other (fringing habitat)	22 (44%)
Perches (fringing habitat)	16 (32%)
*Perches (open water habitat)	14 (28%)
*Other (open water habitat)	14 (28%)
Drains	2 (4%)
Mangroves	n/a

* = open water habitat sub-units. . n/a = not applicable to the estuary.

corded in the estuary). They were also used for roosting (18.3%), which mainly took place on the sandbars, on perches within the open water and to a lesser extent on the tidal flats. Loafing (7.8%) mainly took place in the deep water basin and shallow water (Table 3). In contrast, the fringing wetlands together supported 7 019 waterbirds (33% of total waterbirds recorded) comprising 46 species (92% of all species recorded). Since the fringing wetlands only comprise approximately 11% of the estuary, these facts reveal a disproportionately high use of this small wetland area (24 birds ha^{-1}) compared to the rest of the estuary (6 birds ha^{-1}). The fringing wetland sub-units were mainly used for roosting (16.8% of behavioural activity recorded in the estuary) and feeding (12.3%). Bare shoreline, perches and wet and dry salt marsh were favoured for roosting and bare shoreline, wet salt marsh and pools were favoured for feeding (Table 3). Most habitats throughout the estuary supported a range of species; most notably the wet salt marsh supported 78% of all species recorded in the estuary (Table 4).

In the out-lying wetlands, the open water habitats had 23% of the 2 525 waterbirds recorded in these wetlands, comprising 22 species (54% out of 41). These sub-units were used mainly for a mixture of feeding, roosting and to a lesser extent, loafing (Table 5). By contrast 77% of the waterbirds recorded were found in fringing wetland habitat sub-units, mainly the pools, perches and 'other' sub-units (Table 5). These comprised 36 species (88% of species recorded). These habitats were used mainly for feeding and roosting. Notably the pools in the fringing wetland habitat alone supported 61% of species. They were used mainly for feeding with some loafing (Tables 5, 6). A significant amount of breeding activity was noted in the perches and to a lesser extent the pools (Table 5).

Species protected by international migratory bird agreements

The Federal Government of Australia is committed to the protection of a number of migratory waterbirds through the Japan-Australia Migratory Agreement (JAMBA) and the China-Australia Migratory Bird Agreement (CAMBA). In the Leschenault Inlet estuary 6 385 waterbirds comprising 17 species scheduled under international migratory bird agreements were recorded. The out-lying wetlands supported nine of these species. While the out-lying wetlands did not contribute any additional species under migratory bird agreements they contributed 289 (4.3% from a total of 6 674) additional waterbird records for these species.

In the Leschenault Inlet estuary the tidal flats appear to be particularly important to these species, as there were more than double the number of waterbirds present in this habitat sub-unit compared to other sub-units. The tidal flats, wet salt marsh, bare shoreline, shallow water and sandbar sub-units support 88% of these species (Table 7). The wet salt marsh sub-unit is also highly significant because it supports 100% of these species recorded in the Leschenault Inlet estuary (Table 8).

In the out-lying wetlands the tidal flats, wet salt marsh and shallows were also important, but not the bare shoreline and sandbars. Perches and other elements in the fringing habitat were important. Together the five sub-

Table 5. Habitat sub-units of the out-lying wetlands ranked by abundance of waterbirds. Major behavioural activities in each sub-unit are also presented in order of prominence.

Habitat Sub-Units in Out-lying wetlands	Number of Birds & % Abundance	Major Activity Types
Pools (fringing habitat)	654 (25.9%)	Feed, Loaf
Other (fringing habitat)	442 (17.5%)	Roost, Feed
Perches (fringing habitat)	438 (17.3%)	Roost, Breed
Wet salt marsh	225 (8.9%)	Roost, Feed
*Shallow water	213 (8.4%)	Feed, Loaf
*Tidal flats	134 (5.3%)	Feed, Roost
*Sandbars	88 (3.5%)	Roost
*Perches (open water habitat)	78 (3.1%)	Roost
Bare shoreline	71 (2.8%)	Roost
Mangroves	68 (2.7%)	Feed
*Deep water basin	48 (1.9%)	Loaf, Feed
Dry salt marsh	40 (1.6%)	Roost
Drains	16 (0.6%)	Roost
*Other (open water habitat)	10 (0.4%)	Roost, Fly

* = open water habitat sub-units.

Table 6. Habitat sub-units of the out-lying wetlands ranked by richness of waterbird species.

Habitat Sub-units in Out-lying Wetlands	Species Richness & % Total Species	
Pools	25	(61.0%)
Other (fringing habitat)	21	(51.2%)
Wet salt marsh	16	(39.0%)
Bare shoreline	15	(36.6%)
Perches (fringing habitat)	13	(31.7%)
Mangroves	12	(29.3%)
*Shallow water	11	(26.8%)
*Deep water basin	8	(19.5%)
*Tidal flats	8	(19.5%)
Drains	7	(17.1%)
*Sandbars	6	(14.6%)
*Perches (open water habitat)	5	(12.2%)
Dry salt marsh	4	(9.8%)
*Other (open water habitat)	2	(4.9%)

* = open water habitat sub-units.

Table 7. Habitat sub-units of Leschenault Inlet estuary ranked by the abundance of waterbirds protected by international migratory bird agreements.

Habitat Sub-units in Estuary	Number of Birds & % Abundance	
*Tidal flats	1999	(31.3%)
Wet salt marsh	993	(15.5%)
Bare shoreline	961	(15.0%)
*Shallows	838	(13.1%)
*Sandbars	815	(12.8%)
Dry salt marsh	221	(3.5%)
Pools	109	(1.7%)
Other (fringing habitat)	85	(1.3%)
*Deep water basin	31	(0.5%)
Perches (fringing habitat)	8	(0.1%)
*Perches (open water habitat)	4	(0.06%)
*Other (open water habitat)	1	(0.01%)
Drains	0	
Mangroves	n/a	

* = open water habitat sub-units. n/a = not applicable

Table 8. Habitat sub-units of the Leschenault Inlet estuary ranked by the richness of waterbird species protected by international migratory bird agreements.

Habitat Sub-units in Estuary	Species Richness & % Total Species	
Wet salt marsh	17	(100%)
Bare shoreline	13	(76%)
Pools (fringing habitat)	12	(70.5%)
*Tidal flats	12	(70.5%)
*Sandbars	10	(58.8%)
*Shallows	10	(58.8%)
Dry salt marsh	7	(41.1%)
*Deep water basin	5	(29.4%)
Perches (fringing habitat)	2	(11.8%)
*Perches (open water habitat)	2	(11.8%)
*Other (open water habitat)	2	(11.8%)
Other (fringing habitat)	4	(23.5%)
Drains	0	
Mangroves	n/a	

* = open water habitat sub-units. n/a = not applicable

Table 9. Habitat sub-units of the out-lying wetlands ranked by the abundance of waterbirds protected by international migratory bird agreements.

Habitat Sub-units in Out-lying Wetlands	Number of Birds & % Abundance	
Wet salt marsh	70	(24.2%)
Perches (fringing habitat)	52	(18.0%)
*Tidal flats	48	(16.6%)
*Shallows	44	(15.2%)
Other (fringing habitat)	37	(12.8%)
Pools	17	(5.9%)
Mangroves	12	(4.1%)
Drains	4	(1.4%)
Bare shoreline	3	(1.0%)
*Sandbars	2	(0.7%)
*Other (open water habitat)	0	
Dry salt marsh	0	
*Deep water basin	0	
*Perches (open water habitat)	0	

* = open water habitat sub-units.

Table 10. Habitat sub-units of the out-lying wetlands ranked by the richness of waterbird species protected by international migratory bird agreements.

Habitat Sub-units in Out-lying Wetlands	Species Richness & % Total Species	
Wet salt marsh	5	(55.5%)
*Tidal flats	5	(55.5%)
Pools (fringing habitat)	3	(33.3%)
Mangroves	3	(33.3%)
*Shallows	3	(33.3%)
Other (fringing habitat)	3	(33.3%)
Bare shoreline	2	(22.2%)
Drains	2	(22.2%)
*Sandbars	2	(22.2%)
Perches (fringing habitat)	1	(11.0%)
Dry salt marsh	0	
*Deep water basin	0	
*Perches (open water habitat)	0	
*Other (open water habitat)	0	

* = open water habitat sub-units.

units having the most waterbirds supported 86.8% of all the waterbirds recorded (Table 9). The wet salt marsh notably supported 55% of species scheduled under international migratory bird agreements, in the out-lying wetlands (Table 10).

Breeding species

In the Leschenault Inlet estuary, 124 waterbird records involved evidence of breeding (29% from a total of 432 breeding records in the estuary and out-lying wetlands combined) involving six species (37.5% from a total of 16 breeding species). These observations mainly involved recently hatched young feeding. The out-lying wetlands contributed 308 additional records of breeding behaviour (71%) providing 10 extra species (62.5%). Species displaying breeding behaviour are noted in the Appendix.

As there were few breeding observations made in the Leschenault Inlet estuary compared to the out-lying wetlands, the analysis of habitat use by breeding birds is assessed using the combined data from the estuary and out-lying wetlands. In the estuary and out-lying wetlands evidence of breeding was found from June to December, but was not evident in the mid summer to late autumn surveys. Ninety percent of all breeding activity occurred in the August to October surveys. Breeding activity occurred mainly at Marriot Road Swamp site 25 (55%), site 32 (13%), La Porte Swamp site 17 (7.2%), site 22 (5.5%) and site 12 (4.9%). Notably site 12 has been destroyed in the course of development.

In the estuary and out-lying wetlands breeding activity occurred predominantly in the fringing wetland habitat, which contained 85% of all waterbirds exhibiting evidence of breeding. In particular the perches in the fringing wetlands had 49% of the breeding records (Table 11). The fringing wetland habitat also supported 100% of the species exhibiting breeding behaviour. In particular the pools and perches in the fringing wetland habitat supported 50% and 44% of species displaying breeding activity respectively. By contrast the open water habitat only supported 12.5% of species exhibiting breeding behaviour or evidence of breeding. These observations largely comprised young feeding (Table 12).

A State perspective of Leschenault Inlet estuary

The Birds Australia data bank (Anon 1999) containing the results of broad-scale waterbird surveys of over 700 wetlands in southern Western Australia was consulted. These wetlands, both tidal and freshwater, are located from Kalbarri to Esperance. According to these data, Leschenault Inlet estuary ranked highly for its importance to waterbirds under many parameters. The estuary ranks in the top 5% of wetlands of importance to waterbirds in terms of species richness, richness of species scheduled under international migratory bird agreements and median numbers of waterbirds. The estuary also ranks in the top 10% of wetlands in terms of numbers of waterbirds scheduled on international migratory bird agreements and in the top 15% for maximum numbers of waterbirds counted in any one survey. It is also ranked in the top 1% of wetlands of importance for numbers of Caspian Tern (*Sterna caspia*) and in the top 5% of wetlands of importance for numbers of Australian Pelican (*Pelecanus conspicillatus*), Little Pied Cormorant (*Phalacrocorax melanoleucos*), Darter (*Anhinga melanogaster*), Australian Shelduck (*Tadorna tadornoides*), Common Greenshank (*Tringa nebularia*), Red-necked Stint (*Calidris ruficollis*), Pied Oystercatcher (*Haematopus longirostris*), Crested Tern (*Sterna bergii*) and Silver Gull (*Larus novaehollandiae*). Site 12, in the out-lying wetlands, was ranked in the top 5% of wetlands of importance to the Australian Wood Duck (*Chenonetta jubata*) before it was destroyed by development.

Some of the out-lying wetlands were not included in the Birds Australia data bank. When data on these wetlands (Ninox Wildlife Consulting 1989) were compared with data from Birds Australia, Marriot Road Swamp (site 25) ranked in the top 5% of wetlands of importance to waterbirds in terms of richness of breeding species.

Discussion

Functional use of habitats within the Leschenault Inlet
estuary area.

The habitat usage and behavioural activity data presented here were collected for all seasons within a 14-month period. Sampling was conducted during the day only. A three to four year data collection, including data gathered in both wet and dry years, and data gathered at night, would be preferable. This would help deduce how waterbirds use the estuary and out-lying wetlands under different annual conditions and in the evening. However, as this type of habitat and activity data are rarely gathered, the data analysed in the present study still provide a valuable insight into the relative uses of wetland habitat by waterbirds.

Based on this 14-month study of habitat usage in the wider Leschenault Inlet estuary area, it was determined that waterbirds made extensive use of most habitats within the estuary and out-lying wetlands, but often used them for different purposes. In the estuary the majority of waterbirds, comprising a large variety of species, use the open water habitats. These habitats are largely used for feeding and to a lesser extent for roosting or loafing. By contrast only one third of waterbirds use the fringing wetlands. However, they concentrate into a much higher density over this small wetland area, suggesting that some of these habitat sub-units provide important resources for waterbirds. Notably a huge variety of species (92% of all species counted) use the fringing wetlands, which are used equally for roosting and feeding.

In the out-lying wetlands the preferences for habitats appears to be reversed. The majority of waterbirds and the majority of species use the fringing wetland habitat sub-units. These habitats are used mainly for feeding and roosting and to a lesser extent for breeding. However, as there is less open water habitat in the out-lying wetlands, this apparent reversal in preference would not be as pronounced as the results of the surveys suggest.

Table 11. Habitat sub-units of the Leschenault Inlet estuary and out-lying wetlands ranked by the abundance of waterbirds exhibiting evidence of breeding.

Habitat Sub-units	Number of Birds & % Abundance	
Perches (fringing habitat)	213	(49.3%)
Pools (fringing habitat)	92	(21.3%)
*Deep water basin	48	(11.1%)
Wet salt marsh	36	(8.3%)
'Other' (fringing habitat)	18	(4.2%)
*Shallow water	17	(3.9%)
Dry salt marsh	7	(1.6%)
*Perches (open water habitat)	1	(0.2%)

* = open water habitat sub-units.

Table 12. Habitat sub-units of the Leschenault Inlet estuary and out-lying wetlands ranked by the richness of species exhibiting evidence of breeding.

Habitat Sub-units	Species Richness & % Total Species	
Pools (fringing habitat)	8	(50.0%)
Perches (fringing habitat)	7	(43.7%)
Wet salt marsh	3	(18.7%)
Other (fringing habitat)	3	(18.7%)
*Shallow water	2	(12.5%)
Dry salt marsh	1	(6.2%)
*Deep water basin	1	(6.2%)
*Perches (open water habitat)	1	(6.2%)

* = open water habitat sub-units.

Some habitat sub-units shared similar waterbird usage patterns, while others had their own distinctive characteristics. The waterbird usage and likely conservation value of each sub-unit is summarised below.

Deep water basin, shallow water, tidal flats and sandbars. The deep water basin, shallow water, tidal flats and sandbars in Leschenault Inlet estuary appear to have similar functional uses. They are all favoured by a large number and variety of waterbirds and together support 58% of all waterbirds recorded in the estuary. These habitat sub-units are used mainly for feeding and resting (roosting and loafing). The shallower sub-units (tidal flats, sandbars and shallow water) also attract a large number and variety of waterbird species scheduled under international migratory bird agreements, mainly comprising small shorebirds. The tidal flats are particularly favoured by migratory shorebirds for feeding. In the out-lying wetlands these habitat sub-units are characterised by relatively small numbers of waterbirds and a smaller variety of species, consistent with the smaller area they occupy. All habitats are used for feeding and resting except for the sandbars, which are only used for roosting. The deep water basin and shallows supported small numbers of feeding young, which would have hatched nearby. The deep water basin, shallow water, tidal flat and sandbar habitat sub-units appear to have very important conservation value to waterbirds in both the estuary and out-lying wetlands.

Wet salt marsh, bare shoreline and pools. In the estuary, the wet salt marsh, bare shoreline and pools all attract a large variety of waterbirds in large-moderate numbers, including a large variety of species scheduled under international migratory bird agreements. The wet salt marsh and bare shoreline also attract high numbers of these migratory waterbirds. Waterbirds mainly feed and rest (roost or loaf) in these habitats. During hot, dry summers waterbirds may utilise the fresh water seeps. The fresh water comes from ground water mounds under the dunes of Leschenault Peninsula. It discharges into the western side of the estuary, diluting the tidal pools and attracting a variety of waterbirds (Cresswell 2000). In the out-lying wetlands the pools, wet salt marsh and bare shoreline habitat sub-units are characterised by relatively smaller numbers of waterbirds, consistent with the smaller area they occupy, but a large variety of species. However, they attract only a small variety and number of species scheduled under international migratory bird agreements. The wet salt marsh and pools also attract small numbers of a moderate variety of waterbirds, which utilise them for breeding activity. These three habitat sub-units appear to have significant conservation value to waterbirds in both the estuary and out-lying wetlands.

Dry salt marsh. In the estuary the dry salt marsh habitat sub-unit attracts a moderate variety of species in small-moderate numbers, including a small variety of species scheduled under international migratory bird agreements in moderate numbers. This habitat is used almost entirely for roosting. In the out-lying wetlands the dry salt marsh habitat has a similar function, but much smaller numbers and variety of waterbirds use it and no species scheduled under international migratory bird agreements were found there. When this supra-tidal area is inundated it presumably assumes the same functional uses as the wet salt marsh and its conservation value would shift from moderate to high.

Mangroves. The mangroves in the out-lying wetlands are used by a small variety of species in small numbers for feeding. Considering that this habitat sub-unit was only recognised at one sample site (site 40) in this study, and is a very small in area, it is likely to be of greater importance to waterbirds than the surveys suggest. Notably, during the dry season site 40 was used as a dry season refuge by many waterbirds. The small mangrove areas in the estuary, which were lumped with other sub-units in the present study, may be used similarly. Mangroves are likely to be of moderate conservation value to waterbirds.

Drains. The drains transverse through a variety of habitats in the fringing wetlands. In the estuary and out-lying wetlands, they are used by a very small number and variety of waterbirds, but appeared to be a little more used in the out-lying wetlands. Based on the findings of Storey *et al.* (1993), who investigated waterbird usage in many types of wetlands, they are likely to have low conservation value to waterbirds.

Perches in fringing and open water habitats. In the estuary, perches attract a moderate variety of species in moderate numbers. Considering these habitat elements comprise a minute proportion of the areas sampled in the estuary (fence post protruding out of the water, edges of paper bark thickets that were easily visible to the observer, dead trees *etc.*), waterbirds show strong disproportionate preference for them for roosting. They are similarly favoured in the out-lying wetlands, where they are also used for breeding. Perches supported 50% of all waterbirds exhibiting evidence of breeding including many colonial nesting species. Perches would appear to be important habitat elements in the estuary and out-lying wetlands, and of particularly high conservation value when they support breeding.

'Other' habitat in the fringing wetlands. The 'other' fringing wetland habitat sub-unit is a miscellaneous category comprising roads, car parks, grassed areas, fly-ash dumps and telephone poles. In the estuary these habitat elements together support roosting activity in a moderate variety of waterbirds, in small-moderate numbers. These were predominantly Silver Gull (*Larus novaehollandiae*) using grassed areas and car parks. In the out-lying wetlands they support both roosting and feeding in a moderate variety and number of waterbirds including a small variety and number of species scheduled under international migratory bird agreements. These were mainly Great Egrets (*Ardea alba*). Small low-lying grassed areas can be a useful compliment to adjacent wetland conservation areas, particularly when wet, as they will readily be used by ibis, gulls, lapwings and some duck species for feeding. If they contain large mature trees with hollows, these may also be used by ducks for breeding and egrets, herons and wetland raptors for perching.

Role of Leschenault Inlet estuary

Waterbirds are generally very mobile using a wide network of wetlands and wetland habitats to provide them with the necessities of life. In southern Western Australia, a given waterbird may utilise different wetlands for feeding, roosting or breeding on the same day. While the availability of food and suitable breeding and roosting habitat and migration routes are probably the ultimate determinants of waterbird distribution at any given time, waterbird abundance correlates with wetland size, depth, vegetation structure, primary productivity and rainfall via its effects on food production and provision of fresh water for young to drink (*e.g.* Frith 1967; Jaensch *et al.* 1988; Storey *et al.* 1993).

The results of the present study, and the large-scale survey data gathered by Birds Australia, together suggest that the Leschenault Inlet estuary is an important waterbird habitat within southern Western Australia and is likely to be a critical integral component of the wetland network used by waterbirds in the south-west. The estuary is one of the largest waterbodies in southern Western Australia (2 600 ha) and is permanent. It attracts a very large and rich waterbird fauna throughout the year. The greatest numbers of waterbirds occur in mid spring and summer, suggesting it is used as a dry season refuge at these times when many coastal and inland wetlands are dry. It is significant to species scheduled under international migratory bird agreements, supporting a high richness of these species in significant numbers particularly in spring and summer. In summer and autumn many migrant shorebirds leave. More waterbirds leave in autumn after autumn rain has occurred on the coastal plain and inland. They presumably leave to take advantage of food resources on these freshly wet areas. However, even in winter, when numbers of waterbirds are reduced, the estuary has still supported over 1 000 waterbirds comprising at least 24 species. As a result the estuary ranks in the top 5% of ranked wetlands in southern Western Australia in terms of median numbers of waterbirds, reflecting its constant use. While the estuary itself supports few nesting waterbirds, most observations on breeding behaviour suggest that it provides a food source for young that have been largely hatched in the nearby out-lying wetlands and perhaps elsewhere.

The out-lying wetlands appear to be a complementary part of a wider wetland network. Ornithologically speaking the Leschenault Inlet estuary and out-lying wetlands appear to be complementary parts of the same wetland system. Although the out-lying wetlands support smaller numbers of waterbirds, they support five species that have never been recorded in the Leschenault Inlet estuary (Appendix). They support most waterbirds in mid spring decreasing into winter. Most of the out-lying wetlands are deserted in the dry season, however three sites support waterbirds throughout the year. Most notably, site 40 supported more than a hundred waterbirds during each survey conducted in the dry season. The out-lying wetlands are also important for breeding activity. They supported the majority of waterbirds exhibiting evidence of breeding and the majority of breeding species recorded in the Leschenault Wetland System during the present study. The most notable wetland for breeding waterbirds is Marriot Road Swamp (site 25) which has supported 55% of all breeding in the area. Breeding takes place in the Leschenault Wetland System between June and December, with 90% of it occurring in August to October. It is likely that many waterbirds hatched in the out-lying wetlands feed and grow in the nearby estuary, however only mark and recapture techniques could resolve this question.

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Appendix

Waterbird species recorded on the Leschenault Inlet estuary and out-lying wetlands during the surveys by Ninox Wildlife Consulting (1989). *Breeding Species. +Species recorded in the out-lying wetlands only. # Species scheduled on international migratory bird agreements. Nomenclature and order follow Christidis & Boles (1994).

ANATIDAE		
	Musk Duck	*Biziura lobata*
*	Black Swan	*Cygnus atratus*
*	Australian Shelduck	*Tadorna tadornoides*
*	Australian Wood Duck	*Chenonetta jubata*
*	Pacific Black Duck	*Anas superciliosa*
	Australasian Shoveler	*Anas rhynchotis*
*	Grey Teal	*Anas gracilis*
PODICIPEDIDAE		
*	Australasian Grebe	*Tachybaptus novaehollandiae*
	Hoary-headed Grebe	*Poliocephalus poliocephalus*
ANHINGIDAE		
	Darter	*Anhinga melanogaster*
PHALACROCORACIDAE		**be**
*	Little Pied Cormorant	*Phalacrocorax melanoleucos*
*	Pied Cormorant	*Phalacrocorax varius*
*	Little Black Cormorant	*Phalacrocorax sulcirostris*
	Great Cormorant	*Phalacrocorax carbo*
PELECANIDAE		
	Australian Pelican	*Pelecanus conspicillatus*
ARDEIDAE		
*	White-faced Heron	*Egretta novaehollandiae*
	Little Egret	*Egretta garzetta*
	White-necked Heron	*Ardea pacifica*
*#	Great Egret	*Ardea alba*
+	Nankeen Night Heron	*Nycticorax caledonicus*
THRESKIORNITHIDAE		
*	Australian White Ibis	*Threskiornis molucca*
	Straw-necked Ibis	*Threskiornis spinicollis*
*	Yellow-billed Spoonbill	*Platalea flavipes*
ACCIPITRIDAE		
	Osprey	*Pandion haliaetus*
	Swamp Harrier	*Circus approximans*
RALLIDAE		
*	Buff-banded Rail	*Gallirallus philippensis*
	Spotless Crake	*Porzana tabuensis*
+	Purple Swamphen	*Porphyrio porphyrio*
*+	Dusky Moorhen	*Gallinula tenebrosa*
+	Eurasian Coot	*Fulica atra*
SCOLOPACIDAE		
#	Black-tailed Godwit	*Limosa limosa*
#	Whimbrel	*Numenius phaeopus*
#	Eastern Curlew	*Numenius madagascariensis*
#	Common Greenshank	*Tringa nebularia*
#	Common Sandpiper	*Actitis hypoleucos*
#	Grey-tailed Tattler	*Heteroscelus brevipes*
#	Ruddy Turnstone	*Arenaria interpres*
#	Great Knot	*Calidris tenuirostris*
#	Red Knot	*Calidris canutus*
#	Red-necked Stint	*Calidris ruficollis*
#	Sharp-tailed Sandpiper	*Calidris acuminata*
#	Curlew Sandpiper	*Calidris ferruginea*
HAEMATOPODIDAE		
	Pied Oystercatcher	*Haematopus longirostris*
RECURVIROSTRIDAE		
	Black-winged Stilt	*Himantopus himantopus*
	Banded Stilt	*Cladorhynchus leucocephalus*
	Red-necked Avocet	*Recurvirostra novaehollandiae*
CHARADRIIDAE		
#	Pacific Golden Plover	*Pluvialis fulva*
#	Grey Plover	*Pluvialis squatarola*
	Red-capped Plover	*Charadrius ruficapillus*
#	Greater Sand Plover	*Charadrius leschenaultii*
	Black-fronted Dotterel	*Elseyornis melanops*
+	Banded Lapwing	*Vanellus tricolor*
LARIDAE		
	Silver Gull	*Larus novaehollandiae*
#	Caspian Tern	*Sterna caspia*
	Crested Tern	*Sterna bergii*
	Fairy Tern	*Sterna nereis*
SYLVIIDAE		
	Little Grassbird	*Megalurus gramineus*